

**ROLE PLAYED BY MIMA MOUNDS IN THE FEEDING DYNAMICS
OF HERBIVOROUS MAMMALS IN NAIROBI NATIONAL PARK**

A thesis submitted in partial fulfilment for the degree of Master of Science (Biology of Conservation) in the University of Nairobi.

By

John M. Waithaka

1988

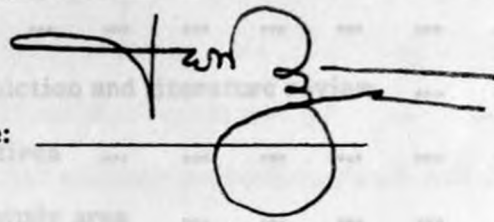
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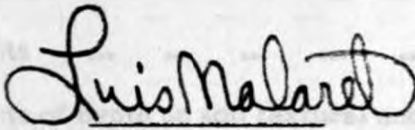
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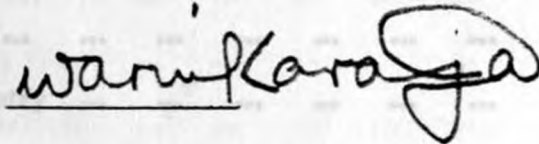
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ACKNOWLEDGEMENTS

Thanks are due to the study team from the National Science Foundation - California Station, through Professor George W. Cox. Prof. Cox was helpful in many ways before the study began, was instrumental in organizing my work and provided many suggestions during and after the field work. I am most grateful to Dr. Lutz Malaret and Dr. Ward Bond for their assistance in the field. They were inspiring, offered suggestions and constructive criticisms during the time of study and when preparing the thesis. Together with Dr. J.J. Rehrer, I wish to thank them most sincerely for their assistance and guidance.

On several occasions I was accompanied by my wife, Wjort, who shared with me the excitement and excitement of viewing animals at dawn, and who lighted my way through the night.

I am deeply indebted to Kambodi G.N., Vachira M.M., Chacha E.N., among others for their encouragement, concern, hospitality and patience. Finally, I wish to thank Prof. Knott for graciously accepting my chances, Mr. Mathenge of the Safari Department for his help in the field, the drivers from the Zoology Department and all the people who, in one way or the other, made it possible for me to complete the study.

ACKNOWLEDGEMENTS

Financial support for this study came from the National Science Foundation of California, U.S.A. through Professor George W. Cox. Prof. Cox was helpful in outlining research ideas before the study began, was instrumental in acquainting me with field studies and provided many suggestions during and after the field work. For all that he did, I am most grateful. Dr. Luis Malaret and Dr. Warui Karanja were my supervisors in the field. They were inspiring, offered stimulating ideas and constructive criticisms during the time of study and when preparing the thesis. Together with Dr. J.J. Hebrard, I wish to thank them most sincerely for their devotion and guidance.

On various occasions, I was accompanied by my wife, Njeri, who shared with me experiences and excitements of viewing animals at dawn, and who lighted my work in many ways.

I am deeply indebted to Kahindi G.N., Wachira M.M., Chacha E.N. among others for their encouragement, concern, hospitality and patience. Finally, I wish to thank Prof. Kinoti for smoothly controlling my finances, Mr. Mathenge of the Botany Department for his help in the field, the drivers from the Zoology Department and all the people who, in one way or the other, made it possible for me to complete the study.

ABSTRACT

Recent studies of Mima-type earth mounds in Kenya suggest that they differ from adjacent intermound areas in soil texture, plant species composition, primary production and grazing value. This study investigated soil texture, nutrient status and other functional differences between mounds and intermounds within Nairobi National Park during four annual seasons.

Soils on the mounds had more clay and silt but less sand and gravel than those of the intermounds. They had higher cation exchange capacity, higher exchangeable calcium and magnesium and higher pH than intermound soils. Mounds provided more favourable conditions for plant growth than the intermounds.

Mounds supported a more diverse botanical composition, exhibited a lower coverage of grasses of grazing value and forbs, and a greater coverage of shrubs, than intermounds, a pattern indicative of more intense grazing.

Net primary production was higher on the mounds. Death rate of vegetation was higher on the intermounds while decomposition rate of dead vegetation was higher on the mounds during the dry season. The crude protein of the two major grass species and of bulked samples was higher in the mound samples.

Weekly animal counts showed preferential utilization of mound vegetation during the dry season and the exclosure method showed higher grazing harvest on mounds.

CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Mima mounds create a distinctive microtopography in grasslands and savannas of several regions of the world (Cox 1984a). These mounds, made of soil and often containing gravel and small pebbles, are nearly circular in outline and tend towards regularity in spacing (Gakahu and Cox 1984). They range in height from a few centimeters to about 2 metres, in diameter from a few meters to over 50 meters, and in density from several to more than 50 mounds per hectare (Dalquest and Scheffer 1942, Price 1949). They lack internal stratification, are composed of silty or loamy soils and are absent from pure sand or very heavy clay soils (Arkley and Brown 1954). They occur in sites possessing a shallow basement layer such as bedrock, hardpan, claypan or densely bedded gravel. Some authors suggest that they may also be found where a permanent water table impedes drainage, creating waterlogged conditions for prolonged periods and limiting the availability of sites suitable for permanent occupation by burrowing animals.

Numerous hypotheses have been suggested for the origin of these mounds, mostly involving physical processes of soil deposition and erosion (Krinitzsky 1949, Nikiforoff 1941, Dietz 1945, Aten and Bollich 1981, Washburn 1980). Krinitzsky (1949) studied mounds in the Gulf Coast and Washington, U.S.A. and concluded that they were the result of wind and water rearrangement of fluvial material later influenced by vegetation. Nikiforoff (1941) asserted that mounds in California originated from artesian pressure produced by underground water. Mounds found along the Gulf Coast, U.S.A. have also been attributed to water deposition, originating as sandy islets (Dietz 1945). Others (Aten and Bollich 1981) have concluded that rill or stream erosion and entrapment of windblown sediments have resulted in some Gulf Coast mounds. A recent explanation by Washburn (1980) suggested that the mounds in Columbia and Washington were a result of erosion, the pattern of which was determined by seasonal frost.

Some scientists associate mound formation with various glacial processes. Their hypotheses are based on the assumption that the mounded prairies were exposed to periglacial environments during the pleistocene and the mounds are a direct result of processes associated with this environment (Newcomb 1952, Pewe 1948, Ritchie 1953 and McFaul 1979).

The most often cited biological hypothesis, formulated by Dalquest and Scheffer (1942), states that mounds are the gradual product of backward displacement of soil which results from the outward tunneling of pocket gophers (Family Geomyidae) from sites representing territorial centres and the location of permanent nests and food storage chambers. This view has gained support from many scientists (Scheffer 1958, Stallings 1948, Koons 1948, Ross et al. 1968, Murray 1967, Cox 1984a,b,c, Cox and Gakahu 1983, 1985, Cox and Roig 1986, Gakahu and Cox 1984, Cox 1987, Cox et al. 1987). According to this hypothesis, the essential descriptive features of mounds are that they (1) are composed of textural materials that such animals can move; (2) are restricted to thin or poorly drained soils that limit tunneling to a shallow surface zone; (3) are confined to flat or moderately sloping land; (4) are nearly circular in outline regardless of the slope; (5) tend to be evenly spaced because of the strong territoriality of the mole rats and (6) occur only within historic ranges of these animals. There exists no other hypothesis of mound origin with all these characteristics and limitations (Cox 1984).

The rodent implicated with mound formation in Western North America are Geomyid pocket gophers of the genera Geomys and Thomomys. Scheffer (1958) extended the hypothesis to include other groups of fossorial rodents similar to pocket gophers in behaviour and ecology. He suggested that the search for Mima mound microterrain in other regions of the world where such rodents existed was a significant test of the hypothesis. In particular, he suggested that areas in South America, where octodontid and otenomyid gophers occur and parts of Africa where fossorial bathygerid rodents are found, be studied.

In South America, this approach has revealed two localities with mounds, one in the Peruvian Altiplano (Scheffer 1958) and the other in La Pampa, Argentina, where members of another family, the ctenomyid tuco-tucos are present (Cox and Roig 1986). In East Africa, Mima mounds occur in the Kenya highlands (Fries and Fries 1948) (Cox and Gakahu 1983, 1985, Gakahu and Cox 1984) and possibly in northern Tanzania, where Kemp (1955) described mounds very similar to those of the Kenya highlands. The fossorial rodent associated with the East African mounds is the rhizomyid mole rat, Tachyoryctes splendens (Kingdon 1974). Mounds of a similar nature have been reported in various parts of South Africa and are occupied by rodents of the Family Bathyergidae (Merryweather 1965, Van de Merwe 1940, Visser and Schach 1973, Visser and Toerien 1971).

Many of the mounds in Kenya described above have also been attributed to termites (Troll 1936, Glover et al 1964, Jackson and Gartlan 1965, Lind and Morrison 1974, Darlington, 1985 and Lusigi 1977). However, mounds known to be formed by termites differ from those formed by fossorial rodents in many respects. Termite mounds reach heights of one to several meters, are formed of clay rich sub-soil (Pullan 1979) and are richer in clay textural fraction than the adjacent surface soils (Glover et al 1964, Arshard 1981). They also lack pebbles and gravels present in Mima mounds. Termite mounds are largely limited to elevations below 1800 m (Hesse 1955, Pomeroy 1977) while Mima mounds have been recorded at altitudes of 3,500 m on Mt. Kenya (Jarvis and Sale 1971). Termite mounds typically occur in low densities, usually not more than five or six per hectare, are largely bare when active and develop a distinctive vegetation zonation after abandonment due to the highly compacted clay of which the mound is formed (Glover et al, 1964).

The Dalquest-Scheffer hypothesis that Mima mounds in N. America are the long term product of burrowing activities of fossorial rodents was extended to areas of similar topography in Kenya by Cox and Gakahu (1983, 1985). Populations of the rhizomyid mole rat, a fossorial rodent similar in morphology

and social behaviour to the Geomyid pocket gophers, were found associated with the mounds. Mound density and dispersion pattern were found to be similar to features of North American mounds and the distribution of fresh soil heaps indicated that the activities of these animals were mound centred. A shallow laterite hardpan was found underlying all the mounds that were examined. It was concluded that Mima mounds in Kenya were the product of fossorial rodents such as pocket gophers and that these two groups were convergent in morphology, burrowing behaviour and impact on landscape (Cox and Gakahu 1983).

Earlier, Coe (1969) and Jarvis and Sale (1971) had noted the association of mole rats of the genus Tachyoryctes with mounds at high elevations on Mt. Kenya. Coe (1969) suggested that the mounds were formed by burrowing animals. Jarvis and Sale (1971) noted that they might have been formed by other processes and simply colonised by mole rats. They also called attention to the parallel situation with the Mima mounds of western United States.

Studies in Kenya by Cox and Gakahu (1985) indicated that there was a close correspondence between the volume of soil forming the mound and that missing from the adjacent intermound, suggesting that mounds were formed by lateral translocation of soil from intermound to the mound. This finding was in agreement with the descriptive criteria of the Dalquest-Scheffer hypothesis.

T. splendens occurs from Ethiopia southwards and westwards through Kenya and Uganda to Eastern Zaire, Rwanda, Burundi and northern Tanzania (Kingdon 1974). They are seldom found in areas with less than 500 mm annual rainfall and flourish best in upland areas. They can withstand extreme cold, living at altitudes of 3,500 meters on Mount Kenya (Jarvis and Sale, 1971). They favour open grasslands, thinly treed upland savanna, moorland and cultivated areas (Coe 1969, Jarvis and Sale 1971). These mole rats are highly aggressive, the male and female maintaining separate burrow systems (Rahm 1971) which consist of deeply placed nest chambers and extensive exploration and foraging tunnels. Much of the excavated soil is pushed to the surface, forming heaps similar to

those in North America. The mole rats feed on herbaceous plants and shrubs and may become serious farm pests (Rahm 1971).

The controversy of the origin of the mounds of the Thika and Athi plains, within which ecosystem Nairobi National Park lies, started about three decades ago, when, in 1956, Stephen et al. proposed that they were of gilgai origin, having been produced by the cyclical dehydration and rehydration of the very rich clay soils. Later, Scott (1963) considered termite activity as a possible explanation of mound origin but concluded that they did not fully account for it. Ojany (1968) proposed that they originated as lahars, depositions from volcanic mud flows, but later dropped the lahars hypothesis. Cox and Gakahu (1985) studied these mounds and concluded that they were similar to the North American Mima mounds, which, according to many researchers (see above), have been formed by fossorial rodents. They saw the possibility that some of the mounds described by Malaisse (1978), Pullan (1979), Boughey (1965) and other workers, and attributed to termites, were actually mima-type mounds, formed by the activities of fossorial rodents. Darlington (1985) argued against the gilgai and lahar hypotheses, and strongly dismissed the fossorial rodent hypothesis, stating that the apparent similarity between these mounds and those in North America was only superficial. She supported and defended the termite hypothesis of mound origin.

The role of mound-building animals in the origin and maintenance of Mima mounded topography has recently acquired conservational importance. Some areas of mound topography have been designated as nature reserves in California where Mima Mound Natural Area Reserve in Thurston County and Miramar Mounds Natural Landmark in San Diego County are protected. In addition, several preserves have been established in California to protect the distinctive plant and animal communities of vernal pools which typically occur in intermound basins of Mima mound topography (Cox and Gakahu 1983). If Mima mound topography is created and maintained primarily by the activities of animals, this dynamic relationship should be considered in plans for long-term conservation

OBJECTIVES

The general objective is to test whether Mima mounds play a functional role in the herbivore feeding dynamics in grassland ecosystems. The study focusses on the different mound and intermound aspects that influence food availability and utilization by large mammalian herbivores. No detailed study has been made on the dynamic relationship between the herbivores and the vegetation on the mounded grasslands in Kenya (Gakahu and Cox 1985) but many authors have pointed out that mounds possess characteristics that make them more favourable grazing areas than the adjacent intermounds (Scott 1963, Lusigi 1977, Pratt and Gwynne 1977). This study compares various physical and biotic parameters of mounds and intermounds, specifically:

- (1) Soil textural and mineralogical composition;
- (2) Composition of plant species;
- (3) net primary production, death and decomposition rates of vegetation;
- (4) the crude protein of major preferred food plants; and
- (5) time spent by large herbivores grazing.

The findings of this study provide valuable information on the ecology of mounded grasslands and serve as a baseline for follow-up investigations in the attempts to understand our wildlife habitats better.

CHAPTER 2

THE STUDY AREA

Nairobi National Park, established in 1946, covers an area of 114 km² approximately 10 km South of the City of Nairobi, Kenya, and lies about 2° 18' South and 36° 50' East. It is one of the most remarkable parks of its size anywhere in the world since over two dozen big game species which occupy this area are separated from the modern metropolis of Nairobi by a fence.

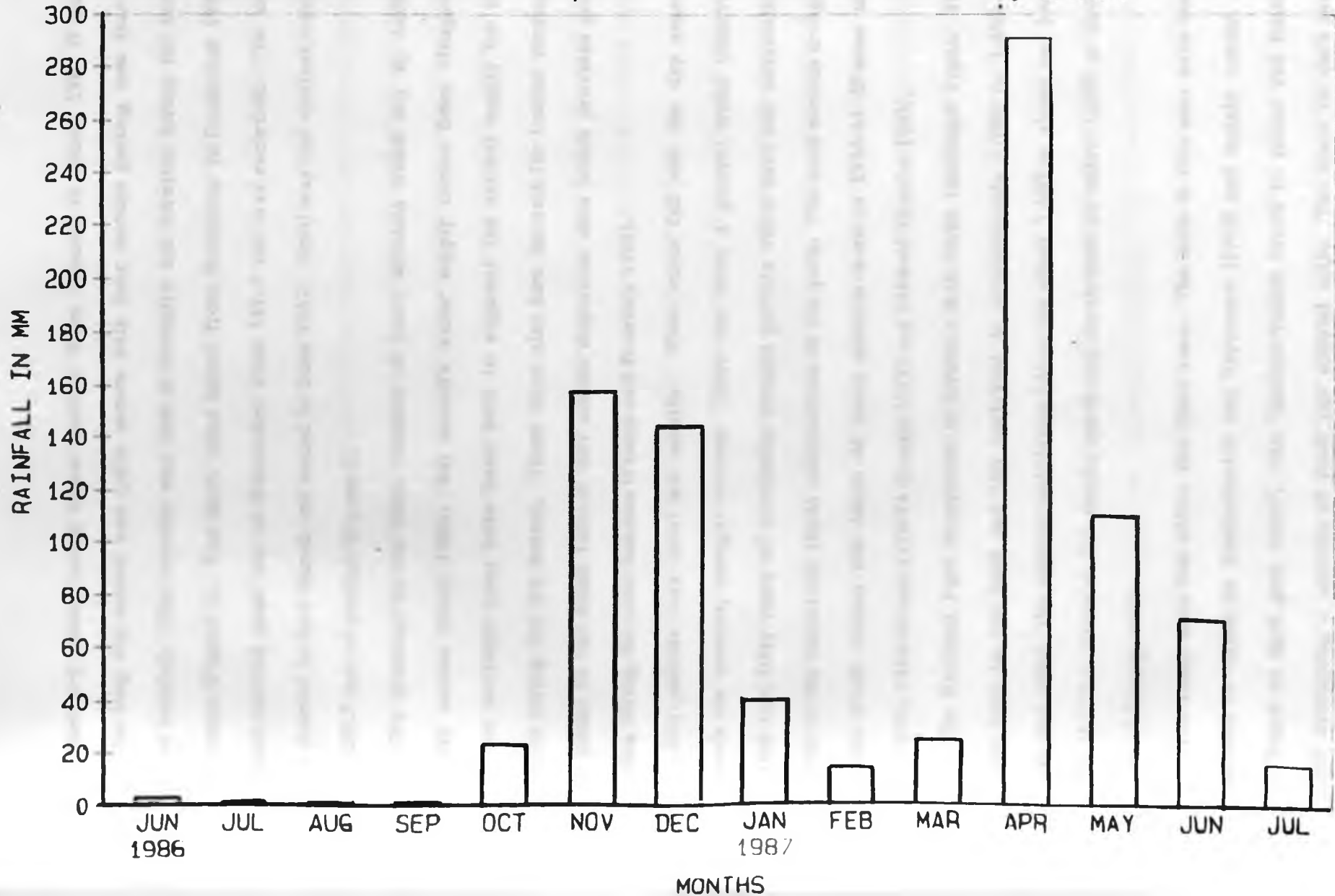
The southern boundary is open to Athi Kapiti plains, which, together with the Park are essentially a part of the same ecosystem and there is considerable movement between the two areas of large ungulate species, notably wildebeests and zebras (Foster and Kearney 1967). The Kitengela Conservation Area which is located to the south of the Park together with the Athi Kapiti Plains form a dispersal area covering about 2,500 km² for many ungulate species (Foster and Kearney 1967). This area is bound to the east by the Nairobi-Mombasa Railway, south by the Nairobi-Magadi Railway, west by the Rift Valley escarpment and north by the settled Nairobi area (Lusigi 1977).

Most of the Park is savanna grassland with a dry climate (Lusigi 1977). The mean annual rainfall for 1955 to 1985 (Kenya Metereological Department Report 1985) is about 850 mm falling mainly in two seasons (long rains from late March to May and short rains from late October to December) but with large variations from year to year.

Rainfall in this area is approximately aligned with an altitudinal gradient with the southern areas receiving less annual rainfall totals than the northern areas (Hillman 1976). This rainfall gradient has been suggested as the main reason for the park being a dry season concentration area for animals (Lusigi 1977).

During the study period there was no deviation from the established rainfall pattern. The long dry season extended from mid-June to late October 1986 while

Figure 1. Rainfall pattern during the study period. (Data obtained from Wilson Airport, 10 km. west of the study area).



the short dry season lasted three months; from January to March 1987 (Figure 1). The long dry season was quite severe with four months getting less than 2 mm of rainfall. This severity was less in intensity and duration during the short dry season (Figure 1). The short rains lasted from November to December 1986. Highest rainfall peak was in November when 157.3 mm was recorded. The long rains started in late March and ended in June 1987. April was the wettest month with 287.7 mm of rainfall (Figure 1).

The drainage in the Park consists of many streams which dry up during the dry season (Scott 1963). All season's water supply comes from Mbagathi River but artificial dams have been built to augment the natural supply for the animals during the dry season. These dams also lure animals for tourist viewing. The plains to the south form a wet season dispersion area which provides good grazing during the rainy seasons (Foster and Kearney 1967).

Dry periods may total six months. When rains fail and the dry season exceeds six months, drought occurs. There has been a general trend observed for the last fifty years of increasing drought periods which have had devastating results on the faunal and floral communities of the park. The most serious drought periods which caused the death of many animals were in 1960-61 (Foster and Coe 1968), 1968-69 and 1973-74 (Lusigi 1977) and 1984-85 (Komba 1985).

The National Park ecosystem is divisible into three landscape types. The upland area to the west and the north-west is approximately 1,700 to 1,800 m above sea level, the central undulating plains are about 1,600 m above sea level while the flat plains of the south, north and north-east lie below 1,600 m above sea level (Lusigi 1977).

The study area lies within the third zone. The soils in this area have been described in detail by Heritz-Smith and Vertcourt (1962) and mainly consist of the "black to dark grey clays", the "shallow-yellow brown to yellow red friable clays" overlaying a laterite of rock and alluvial soils. The black to dark grey clays, commonly known as black cotton soils are the most important in this area.

They go to depths of up to 4 m and are sticky when wet and hard, massive and difficult to break when dry.

Within these soils, there are distinct mounds occupying almost a third of this topographic zone (Lusigi 1977), usually rising to half a meter, with a mean diameter of 20 m. These mounds, which are the subject of this study, vary in size in both horizontal and vertical dimensions. Some are small and can only be detected during the dry season when they get overgrazed and stand out against their less grazed surroundings. Others are quite distinct in size and shape. Most of these mounds seem to be heavily disturbed by grazing, trampling and channelling by burrowing animals. The excavations on the mounds resemble those made by warthogs and aardvarks.

On these mound tops, relics of termite occupation are evident. However, most of them have fresh mole-rat soil heaps interspersed around the mound edges extending outwards into the intermound (the area between mounds).

Trees are very sparse and bushes absent in most of the 180 ha study area except for a small part where shrubs barely 2 meters high, on average, maintained patchy dominance over grass. Heritz-Smith (1962) has given a detailed account of the vegetation in this area. Acacia drepanolobium and A. senegal occur sporadically. Grass species are composed mainly of Pennisetum mezianum, Themeda triandra, Bothriochloa insculpta, Cymbopogon caseus and Digitaria macroblephara. Others common species include Cenchrus ciliaris, Harpachne schimperi, Cymbopogon pospischilii and Sporobolus pellucidus. Found on bare or disturbed grounds are Cynodon dactylon, Eragrostis cilianensis, Aristida adoensis, Digitaria scalarum and Eragrostis tenuifolia. The characteristic herbs include Alysicarpus rugosus, Dolichs sp., Corchurus hochstetteri, Indigofera volkensii and Hibiscus aponeurus, among others.

Nairobi National Park has a concentration of game that while being remarkable, is still only a remnant of the former herds which inhabited the plains some years back (Lusigi 1977). Most of the areas surrounding the Park have

gone to settlement and other human land uses thus causing confinement of animals within the park due to limitation of dispersal routes. The inevitable consequence will be progressive deterioration of the existing habitats which in turn will affect animal distribution and densities.

Large herbivores that are still sufficiently numerous in this habitat include the zebra (Equus burchellii), Grant's gazelle (Gazella granti), Thomson's gazelle (Gazella thomsonii), impala (Aepyceros melampus), waterbuck (Kobus defassa), eland (Taurotragus oryx), kongoni (Alcephalus busephalus), wildebeest (Connochoetes taurinus) and the giraffe (Giraffa camelopardalis). The African buffalo (Syncerus caffer) occasionally occur in large herds but at other times is absent. The park has over 80 recorded mammalian species (Williams 1972) which include small numbers of three species in the vulnerable category of the Red Data Book (Noel 1966), the leopard (Panthera pardus), cheetah (Acynonyx jubatus) and black rhinoceros (Diceros bicornis).

The area is also credited with approximately 500 species of birds, ranging from the Masai ostrich (Struthio camelus), secretary bird, several species of vultures, falcons, kites, eagles, buzzards and bustards to some small birds such as plovers and larks (Williams 1972).

CHAPTER 3

THE SOILS OF THE MOUND AND INTERMOUND AREAS

3.1 INTRODUCTION

Researchers in different parts of the world have pointed out that mound and intermound areas differ in their soil textural and chemical characteristics. Arkley and Brown (1954), McGinnies (1960), Lorio and Hodges (1971), Vitek (1978), and Cox (1984c) have demonstrated this aspect in USA, while Koons (1948), Hesse (1955), Fairburn (1963), Scott (1963), Arshard (1981), Gakahu and Cox (1984) have shown the same trend in East African mounds. Similar observations have been made by Van de Merwe 1940 and Cox et al. 1987 in South Africa. Recent studies on mounds in Argentina by Cox and Roig (1986) have revealed similar results.

No data of soil characteristics on mound and intermound areas has been collected in Nairobi National Park and the adjoining Athi-Kapiti plains. Preliminary observation has shown that mounds in this area are important components of the dynamic interactions between landscape, vegetation and herbivores (Lusigi 1977, Scott 1963, Cox and Gakahu, 1985). The data obtained in this study will provide baseline information that will help to explain differences in vegetation characteristics in mound and intermound areas and differential utilization of vegetation by large mammalian herbivores.

3.2 METHODS

Soil samples were obtained from 4 mound and intermound stations and analysed for differences in their textural and chemical properties. Samples were obtained from four stations which were selected for primary production and plant species composition studies. At each station, triplicate samples were collected from the top of the mounds at depths of 0 - 10 cm, 10 - 20 cm and

40 - 50 cm and from mound-edge and intermound areas at depths of 0-10 cm and 10-20 cm from the surface as soil depth was less than 25 cm. Sampling was done in late March 1987, just at the onset of the long rains in order to establish the textural and nutrient status of the soil at the beginning of a major production period.

Soil analysis was done at the Kenya Soil Survey in the National Agricultural Laboratories. Texture was determined by the hydrometer method in all the 84 samples. Soil reaction (pH) was determined by the electrical conductivity method, Carbon by the Walkley-Black Method, cation exchange capacity (C.E.C.) by leaching with 1N Sodium acetate at pH = 8.2, and exchangeable bases by leaching with ammonium acetate at pH = 7 (Smith and Atkinson 1975).

Differences between mounds and intermounds were tested using one-way analysis of variance.

3.3. RESULTS

3.3.1 Effect of depth on soil textural and chemical properties.

Some soil chemical and physical properties were found to vary at different soil depths. On the mound top gravel was absent from all samples irrespective of sampling depth. There were no differences in sand, silt and clay content or the C.E.C. of the samples taken from depths of 0-10, 10-20 and 40-50 cm. However, pH increased significantly with depth (Table 1). At the mound edge there were no differences in the amount of silt in the 0-10 and 10-20 cm. samples. Clay showed a significant difference (Table I) but sand was evenly distributed along soil depth. There were no significant differences between either C.E.C. or pH at the two soil depths. On the intermounds, texture and C.E.C. were uniform along the soil depth but pH was higher on the surface samples than those obtained 10-20 cm deep. In general, soil texture and C.E.C. levels showed insignificant changes with soil depth in both mounds and intermounds but soil pH decreased with depth in the intermounds, and increased on mounds.

Table 1. The effect of depth on some soil textural and chemical properties
 Degrees of freedom = 2,33 for the mound-top samples and df = 1, 22
 for the mound-edge and intermound samples. Data from the four
 stations are combined (P < 0.05, * = significant).

Sampling Site	Sampling Depth (cm)	X ± sd	n	F
<u>SAND (%)</u>				
Mound top	0-10	29.7 ± 3.39	12	0.282
	10-20	30.5 ± 2.71	12	
	40-50	30.2 ± 2.13	12	
Mound Edge	10-10	39.8 ± 1.59	12	3.00
	10-20	38.7 ± 3.45	12	
Intermound	0-10	43.5 ± 2.80	12	0.119
	10-20	43.2 ± 1.58	12	
<u>SILT (%)</u>				
Mound top	0-10	22.7 ± 2.61	12	1.37
	10-20	22.7 ± 2.46	12	
	40-50	21.5 ± 3.32	12	
Mound Edge	0-10	22.5 ± 1.73	12	1.80
	10-20	18.3 ± 2.06	12	
Intermound	0-10	20.0 ± 2.83	12	0.241
	10-20	19.5 ± 2.11	12	
<u>CLAY (%)</u>				
Mound top	0-10	47.7 ± 4.16	12	0.474
	10-20	46.8 ± 4.13	12	
	40-50	48.2 ± 5.42	12	
Mound Edge	0-10	37.7 ± 2.23	12	31.30*
	10-20	42.8 ± 2.22	12	
Intermound	0-10	36.5 ± 1.93	12	1.29
	10-20	37.3 ± 1.56	12	
<u>PH</u>				
Mound top	0-10	6.8 ± 0.15	12	4.658*
	10-20	7.0 ± 0.32	12	
	40-50	7.1 ± 0.41	12	
Mound Edge	0-10	6.4 ± 0.19	12	2.75
	10-20	6.3 ± 0.09	12	
Intermound	0-10	6.1 ± 0.15	12	6.39*
	10-20	5.9 ± 0.14	12	
<u>GEC (me/100 g)</u>				
Mound top	0-10	29.8 ± 3.89	12	2.014
	10-20	31.9 ± 3.86	12	
	40-50	30.0 ± 3.85	12	
Mound Edge	0-10	24.6 ± 3.10	12	1.18
	10-20	26.2 ± 3.85	12	
Intermound	0-10	21.3 ± 3.43	12	0.041
	10-20	20.2 ± 3.05	12	

Table 2. Mound and intermound soil textural characteristics. Means obtained from mound-top (0-20 cm deep) and intermounds (0 - 20 cm deep) are compared using one way analysis of variance.

Station		$\bar{x} \pm sd$	n	F(3,8)
<u>Gravel (%)</u>				
1	Intermound	68.74 \pm 6.37	3	15.08*
2	Intermound	53.36 \pm 4.45	3	
3	Intermound	40.43 \pm 2.18	3	
4	Intermound	56.46 \pm 6.64	3	
<u>Sand (%)</u>				
				<u>F(1,10)</u>
1	Mound	32.00 \pm 1.79	6	76.83*
	Intermound	40.67 \pm 1.63	6	
2	Mound	31.00 \pm 1.10	6	18.20*
	Intermound	44.67 \pm 1.63	6	
3	Mound	31.00 \pm 1.10	6	22.56*
	Intermound	43.67 \pm 2.34	6	
4	Mound	26.33 \pm 0.82	6	145.28*
	Intermound	44.33 \pm 0.82	6	
<u>Silt (%)</u>				
1	Mound	25.33 \pm 1.63	6	8.00*
	Intermound	22.67 \pm 1.63	6	
2	Mound	21.67 \pm 2.34	6	22.96*
	Intermound	16.67 \pm 1.03	6	
3	Mound	23.00 \pm 2.10	6	9.00*
	Intermound	20.00 \pm 1.26	6	
4	Mound	20.67 \pm 0.42	6	3.46 n.s.
	Intermound	19.67 \pm 0.82	6	
<u>Clay (%)</u>				
1	Mound	42.67 \pm 1.03	6	13.73*
	Intermound	36.67 \pm 1.03	6	
2	Mound	47.33 \pm 1.63	6	120.67*
	Intermound	38.67 \pm 1.03	6	
3	Mound	46.00 \pm 2.19	6	44.25*
	Intermound	36.33 \pm 2.66	6	
4	Mound	53.00 \pm 1.10	6	14.45*
	Intermound	36.00 \pm 0.00	6	

Table 3. The chemical properties of mound and intermound soils. Means of 0-20 cm deep in both areas are compared using one way analysis of variance ($P < 0.05$. ns = not significant).

Station		$\bar{x} \pm$ s.d.	n	F(1, 10)
(i) PH				
1	Mound	6.68 \pm 0.098	6	80.69*
	Intermound	6.00 \pm 0.22	6	
2	Mound	6.80 \pm 0.11	6	93.33*
	Intermound	6.12 \pm 0.13	6	
3	Mound	7.22 \pm 0.29	6	124.32*
	Intermound	5.87 \pm 0.081	6	
4	Mound	6.74 \pm 0.12	6	128.19*
	Intermound	6.02 \pm 0.098	6	
(ii) % NITROGEN				
1	Mound	0.093 \pm 0.028	6	3.33 n.s.
	Intermound	0.120 \pm 0.034	6	
2	Mound	0.10 \pm 0.013	6	0.656 n.s.
	Intermound	0.092 \pm 0.025	6	
3	Mound	0.067 \pm 0.026	6	0.11 n.s.
	Intermound	0.062 \pm 0.025	6	
4	Mound	0.13 \pm 0.017	6	81.67*
	Intermound	0.06 \pm 0.015	6	
(iii) % CARBON				
1	Mound	1.21 \pm 0.13	6	5.65*
	Intermound	1.60 \pm 0.35	6	
2	Mound	1.32 \pm 0.28	6	4.66 n.s.
	Intermound	1.62 \pm 0.20	6	
3	Mound	1.28 \pm 0.20	6	4.35 n.s.
	Intermound	1.10 \pm 0.89	6	
4	Mound	1.19 \pm 0.13	6	7.50*
	Intermound	0.97 \pm 0.15	6	
(iv) G.E.C. (me/100 g)				
1	Mound	27.87 \pm 3.06	6	12.26*
	Intermound	19.33 \pm 5.13	6	
2	Mound	28.53 \pm 2.51	6	23.34*
	Intermound	19.90 \pm 3.58	6	
3	Mound	34.77 \pm 2.58	6	144.90*
	Intermound	21.62 \pm 0.72	6	
4	Mound	32.17 \pm 3.26	6	48.73*
	Intermound	22.15 \pm 1.32	6	

Table 3 cont'd.

Station		$\bar{x} \pm \text{s.d.}$	n	F(1,10)
(v)	<u>EXCHANGEABLE Ca (me/100 g)</u>			
1	Mound	12.55 \pm 1.23	6	77.87*
	Intermound	5.88 \pm 1.37	6	
2	Mound	13.13 \pm 0.96	6	184.89*
	Intermound	5.90 \pm 0.88	6	
3	Mound	16.10 \pm 0.86	6	383.66*
	Intermound	5.58 \pm 0.99	6	
4	Mound	15.00 \pm 1.01	6	175.77*
	Intermound	7.18 \pm 1.03	6	
(vi)	<u>EXCHANGEABLE Mg (me/100 g)</u>			
1	Mound	4.04 \pm 0.69	6	4.44 n.s.
	Intermound	2.79 \pm 1.28	6	
2	Mound	4.27 \pm 0.65	6	12.86*
	Intermound	2.73 \pm 0.84	6	
3	Mound	4.83 \pm 0.50	6	19.80*
	Intermound	2.83 \pm 0.50	6	
4	Mound	4.67 \pm 0.71	6	0.15 n.s.
	Intermound	4.92 \pm 1.41	6	
(vii)	<u>EXCHANGEABLE K (me/100 g)</u>			
1	Mound	1.77 \pm 0.35	6	11.07*
	Intermound	2.29 \pm 0.17	6	
2	Mound	1.72 \pm 0.32	6	13.15*
	Intermound	2.28 \pm 0.21	6	
3	Mound	1.66 \pm 0.45	6	2.40 n.s.
	Intermound	1.97 \pm 0.20	6	
4	Mound	2.26 \pm 0.14	6	5.16*
	Intermound	1.71 \pm 0.28	6	
(viii)	<u>EXCHANGEABLE Na (me/100 g)</u>			
1	Mound	1.13 \pm 0.14	6	7.27*
	Intermound	0.90 \pm 0.15	6	
2	Mound	1.04 \pm 0.26	6	2.50*
	Intermound	0.85 \pm 0.12	6	
3	Mound	0.89 \pm 0.16	6	0.00 n.s.
	Intermound	0.91 \pm 0.22	6	
4	Mound	0.78 \pm 0.18	6	23.45*
	Intermound	1.25 \pm 0.17	6	

*P < 0.05; n.s. = not significant.

3.3.2 Texture

The four textural characteristics of soil varied between mounds and intermound areas. Gravel only occurred in the 10-20 cm deep intermound samples, with significant differences between stations (Table 2). No gravel was found in mound soils even at depths of 50 cm below the surface. Sand occurred in all 84 samples with mean values significantly higher in every intermound in comparison to the the adjacent mound.

Silt was higher in mound soils in three out of four stations and clay content was significantly higher on the mound soils at all four stations.

3.3.3 Soil chemistry

The pH of the soil on the mound top showed a tendency towards neutrality while intermound soils were significantly more acidic (Table 3).

The C.E.C. in mound soils demonstrated higher plant nutrient potential which, on average, was 49% richer than the C.E.C. in intermound soils. The difference was significant.

Analysis of the exchangeable individual cations, % nitrogen and % carbon in the soils gave varying results. Mounds had soils with richer exchangeable calcium than intermounds and magnesium was significantly higher on the mound soils in two out of four stations. Exchangeable sodium and potassium, % nitrogen and % carbon failed to conform to any pattern of distribution between mounds and intermounds.

Discussion

3.4.1 Soil texture

Soil texture is determined by the size of the individual mineral particles as well as the proportion in which they occur. The soil particles are classified as gravel, sand, silt and clay, depending upon size. These textural classes are relatively stable and have considerable influence on soil structure, consistency, degree of compaction and stability, soil drainage, aeration and root penetration

(Landon 1984, Briggs 1981, Jarvis and Jarvis 1972).

The physical, chemical and ecological character of soil depends on texture (Faniran and Areola 1978). The smaller the particles, the larger the total surface area. Chemical weathering increases with increase in surface area and so does the rate of production of plant nutrients. Water-retention capacity also increases along the same gradient because it is partly dependent on the area of wettable surface and partly on capillarity (FitzPatrick 1971, Jarvis and Jarvis 1972).

Gravel, which was found to be a characteristic feature of all intermound areas is known to be poor in nutrients as it has very limited biological activities, low weathering process, insignificant water-holding capacity and low plant nutrient status (Faniran and Areola 1978, Kanwar 1978, Oliver and Boyd 1973). These conditions create a poor environment for plant growth.

Due to the presence of gravel only a few centimeters from the surface, intermound areas possess a shallow layer of top soil with a rooting depth of between 10 and 20 cm. Mounds have much deeper soils ranging above 0.5 m and consequently provided plants with ample rooting depth. On the basis of soil depth alone, mounds would be expected to provide better conditions for plant growth than the adjacent intermounds. The soil depth of the intermound areas in this study agrees with the findings of Cox and Gakahu (1983) in which they found intermound soil depth to be 16 cm. It also conforms to the Dalquest-Scheffer hypothesis (1942) that mounds occur in sites possessing a shallow basement layer such as bedrock, hardpan, claypan or densely bedded gravel.

Sandy soils have good drainage and aeration but yield few plant nutrients because sand has very low chemical activity (FitzPatrick 1971). As the intermound soils were more sandy than mound soils, equal precipitation in the two areas would be expected to percolate down the intermound soil profile much faster than on the mounds. This would have the effect of lowering the amount of water available to intermound plants and would also increase leaching, the results of which would be to impoverish the mineralogical status of the soils.

Mound soils contain more silt and clay than intermound soils. Silt particles are chemically and mineralogically similar to sand, but are smaller in size and contain greater proportions of secondary minerals in their compositions (Faniran and Areola 1978). The importance of silt particles lies in their influence on soil structure and pore space distribution in the soil. (FitzPatrick 1971).

Clay has a high proportion of colloidal particles to which large amounts of water are bound and therefore provides a relatively constant supply of water. It is also able to adsorb more positively charged soil elements and frequently retains them as plant nutrients despite the leaching tendencies of percolating water, making it a valuable reservoir of plant food (FitzPatrick 1971).

The textural conditions of the soils in the two areas show that mounds have better water-retention capacity, ample space for root establishment and a greater ability to store and retain secondary minerals than intermounds. All these factors make mounds more favourable areas for plant growth than intermounds.

These results agree with those of Giles (1970) who demonstrated that soil texture differs between mounds and intermounds with the latter containing higher levels of gravel and sand but less clay. Cox and Gakahu (1985) observed the same soil textural trend in mounds near Kenyatta University, Nairobi.

3.4.2 Soil chemical properties.

The intermound soils were acidic while those from the mounds were almost neutral. Leaching increases with acidity and generally, a combination of acidity and solubility of soil minerals allows a wide range of minerals to be leached, the result of which is to make soils become deficient in plant nutrients (Briggs 1981). Intermound soils are therefore more prone to leaching due to their acidity. The higher level of clay fraction in the mound soils give them a much higher capacity to adsorb cations. Fewer such cations are adsorbed in the intermound clays, a factor that would enhance the rate of leaching and consequently loss

of plant nutrients. The mound and intermound areas would further be expected to show some differences in their plant species composition, especially those with narrow pH requirements, since it is the soil pH that largely determines the chemical environments in which plants live (Stalfelt, 1972).

Calcium in the soil modifies acidity so that it becomes weakly acid, neutral or alkaline as it is a basic cation (Stalfelt 1972). Lower calcium levels in intermound soils may have contributed to low pH while maintaining an opposite effect on the mounds where calcium levels were high. Cox and Gakahu (1985) found the same pH trend in the mound and intermound areas.

The remarkable differences in C.E.C. between mound and intermound soils clearly show that the former have a higher potential for providing plant nutrients. The C.E.C. of the mound soils is rated as high and that of the intermound soils as medium by the F.A.O. C.E.C. scale (FAO 1979). F.A.O. recommends that soils with high C.E.C. are good for agriculture but those with medium values should be used for agriculture with the addition of fertilizer. Del Moral and Deardorff (1976) also found higher C.E.C. values on the mounds of Thurston County, Washington. FitzPatrick (1971) recognises C.E.C. as the only single exchangeable property of the soil which seems to be important for use as a criterion for categorising soils. Russell (1973) gives a word of caution in attaching too much importance to C.E.C. without giving due consideration to levels of individual exchangeable cations. He notes that although the appropriate measurements can give values that, at a given pH, are related to the sum of cations held by the soil colloids, it is an arbitrary value and should only be used as a guide to clay mineralogy. This view is supported by Landon (1984) who argues that knowledge of the level of individual exchangeable cations in a soil are usually of more immediate value in advisory work than the C.E.C. because they indicate the existing nutrient status and can also be used to assess balances among cations.

To supplement the information of the C.E.C. values, the exchangeable cations of the most important base elements were assessed. The F.A.O. (1979) scale rates the exchangeable calcium and magnesium as high on the mounds and medium in the intermounds. Sodium and potassium were high in both areas. There is some indirect evidence of leaching demonstrated by these results. Strong metals like sodium and potassium which cannot be displaced by H^+ maintained equal levels in both mounds and intermounds. Other metals like magnesium and calcium which are not as strongly adsorbed to the clay minerals and can be displaced by H^+ in the process of leaching showed differences. Data on the mound-intermound soil nutrient analysis from McGinnies (1960) shows the same trend, with higher C.E.C., calcium and magnesium levels on the mounds and low potassium levels in both areas. Similar results were obtained by Giles (1970) and Mielke (1977) who found higher levels of plant nutrients in Mima-type mounds than in the adjacent intermound areas.

The levels of nitrogen and organic carbon in both areas is low in the F.A.O. (1979) scale. Nitrogen occurs in the soil in several forms and except in detailed studies, nitrogen measurements are difficult to interpret since the types of nitrogen present and their relevance to plant nutrition are unknown (Landon 1984). It can be deduced, however, that mound soils probably provide richer nitrogen resources than intermounds since the impact of low pH on nitrogen availability is particularly marked in that microbial activity is considerably reduced and available nitrogen is subsequently very low, whatever the total nitrogen (Landon 1984). Landon (1984) further noted that interpretation of nitrogen and carbon as measures of soil fertility are only useful when data on pH is available. Cox and Gakahu (1985) found more organic carbon on the intermounds and Del Moral and Deardorff (1976) found no differences in nitrogen levels between mounds and intermounds.

The higher organic carbon values on the intermounds found by Cox and Gakahu (1985) may be the result of lower grazing intensity on the intermound vegetation. The death and subsequent decomposition of the ungrazed intermound herbage would have the effect of adding organic carbon to the intermound soils. More intense grazing on the mounds brings about the removal of most of the vegetation and consequently should reduce the source of soil organic carbon.

Generally, the concentration of an element in plant tissues is a function of the available nutrient supply such that an increase in supply of nutrients is suggested by the increase in the concentration in the tissues (Kanwar 1978). Kanwar (1978) reported that there exists a curvilinear relationship between the soil nutrient supply and the concentration of an element in the tissue and that there is a direct relationship between the level of specific nutrients in the soil and the primary production in plants. This being the case, mounds should provide better conditions for plant growth than intermounds.

The above hypothesis is based on the fact that the mounds are an area of high productivity. The high rate of vegetation will be a source of the relatively high organic matter input to the soil during the dry season and the rate of decomposition of vegetation will be reduced by the presence of water during the wet season. These hypothetical considerations are essential in attempting to formulate reasons for grazing of the mounds and intermounds of land resources available by livestock on mounds and intermounds.

4.1. Methods

4.1.1. Plant growth measurement

The mounds, grassed and ungrazed were two that the ground top to a grass line below the edge of the mound. A one m² square was located along the perimeter of the mounds at each of the following levels

CHAPTER 4

BOTANICAL CHARACTERISTICS OF MOUNDS AND INTERMOUNDS

4.1 INTRODUCTION

Work already published on mound and intermound vegetation shows that the two areas support a range of different plant species (Del Moral and Deardorff 1976, Mielke 1977, Glover et et 1964, Giles 1970, Cox and Zedler 1986, Cox 1984b). In Nairobi National Park, ^a preliminary survey on the mound and intermound vegetation indicated similar tendencies (Cox and Gakahu 1985).

This phase of the study investigates some aspects of mound and intermound vegetational characteristics such as plant species composition, primary production, crude protein content and its death and decomposition rates. Knowledge of the plant species composition gives the range of food items available to grazers while the primary production is a measure of the quantity of herbage available to herbivores in each season. The crude protein content of vegetation is an index of food quality. The death rate of vegetation will be a measure of the reliability of the mounds and intermounds in providing quality food during the dry season while the rate of decomposition of vegetation will be an indication of the efficiency of nutrient recycling in the two areas. These vegetational characteristics are important in determining the functional responses to grazing and may explain any differential pattern of food resource utilization by herbivores between mounds and intermounds.

4.2 METHODS

4.2.1 Plant species composition

Ten transects, placed 36° apart, were run from the mound top to a point one radius beyond the edge of the mound. A one m² quadrat was located along each transect at the midpoints of each of the following zones:

Mound:	top
	middle
	base
Intermound	1/3 radius from the mound edge
	2/3 radius from the mound edge
	1 radius from the mound edge.

In every quadrat, each species was identified and then categorised into graminoid, forb, sedge or shrub. The percent cover of each species was estimated on an eight-point scale: <1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-99% and >99% (after Cox and Gakahu 1985). This procedure was repeated at six stations to give ten replicates for each station and 60 for each sampling zone. The analysis of variance was used to compare percent cover of graminoids, forbs and shrubs in each mound and intermound and the percent cover of grass species of recognised grazing value on the mounds and intermounds. These grasses were Bothriochloa insculpta, Cymbopogon caseus, Cynodon dactylon, Digitaria macroblephara, D. scalarum and Themeda triandra. Their pasture value has been described by Edwards and Bogdon (1951), Stewart and Stewart (1970), Hoffman (1973) and Sinclair (1977).

The Jaccard's Community Coefficient Index (JCCI) (Jaccard 1928) was used to compare the similarity of the species composition of the mounds and intermounds. This index has relative values that range from 0% when there are no species common to both habitats to 100% when all the species recorded are common to both areas. The formula for calculating this similarity is shown below:

$$JCCI = (c / (a + b + c)) \times 100$$

where a = species unique to one habitat

b = species unique to the other habitat

c = species shared by both habitats

JCCI larger than 50% indicate close similarity in species composition between the two areas while a smaller value indicates that the two areas are

different.

The frequency distribution of plant species occurring in all the six mound-intermound stations was tested for randomness using the Runs Test (Wonnacott and Wonnacott 1976).

4.2.2 Plant production and their death and decomposition rates

Estimates of the net above ground primary production and consumption by large mammalian grazers were made within and outside exclosures on four representative mound and intermound stations. The four stations were randomly selected by use of random number tables from ten stations, each containing a mound with a diameter greater than 15 metres to allow enough space for seasonal shifting of exclosures, a distance from the nearest mound greater than 30 m to minimise any influence a mound may have on its adjacent intermound area, a height of 0.5 m and exhibited evidence of mole-rat activity.

In each station, an exclosure, 1.5 x 1.5 m was set on the mound and intermound areas. Nine 0.1 m² plots were placed inside each exclosure for three replicated samples during a given season of (i) initial live and dead biomass (ii) final live and dead biomass and (iii) final dead biomass plots from which all live matter had been removed at the start of the season. Outside the exclosure, six 0.1 m² plots were designated for similar replicated sampling of (i) and (ii) above. The plots were clipped at the beginning and end of each of the four seasons (long and short rains; long and short dry season). After the final clippings at the end of a season were made, the exclosure were shifted within the same mound-intermound station, plots established and grass clipped to provide the initial data for the next season. Plots inside exclosures provided data on the rates of primary production, death of live tissue and decomposition of dead plant matter. When compared with plots outside the exclosures, the amount of vegetation grazed during each season was obtained.

Clipped samples of plant materials were oven-dried at 80°C for 48 hours and weighed. This sampling procedure enabled the use of the technique used by Wiegert and Evans (1964) for evaluating primary production. This method corrects for loss of shoot material by death and decomposition and assumes a gradual change in standing crop values between periods of measurement. Forage consumption by grazers was estimated using the method of Cox and Waithaka (in press).

4.2.3 Crude protein content of mound and intermound vegetation.

Crude protein, one of the main nutritive constituents of grass, was used to compare the grazing value of species occurring on mounds and intermounds. Samples of Themeda triandra and Bothriochloa insculpta, the two grass species of recognised grazing value with the highest frequency of occurrence were collected in early January 1987 during the short rainy season's growth peak from the mound top and at a distance of one radius from the mound edge.

A transect was established from the mound top into the intermound by randomly selecting one of the four main compass directions and the nearest grass species of interest was clipped at ground level, carefully separated from other species growing in association and placed in a thick plastic bag. This procedure was repeated three times for each grass species in each sampling area. Bulked samples were also obtained by collecting samples of every species occurring in 1 m² quadrat along a transect determined as explained above. Three replicates were obtained for each area.

All samples were labelled, and taken to Kenya Agricultural Laboratories for analysis. Nitrogen was determined using the Kjeldahl procedure and crude protein was obtained by multiplying the results by 6.25 (Lyttleton 1973). The data for mounds and intermounds were compared using one-way analysis of variance.

4.3 RESULTS

4.3.1 Plant species composition

A total of 141 species (see appendix) were recorded within the six mound-intermound stations: 44 were restricted to the mounds, 22 to the intermounds and 75 were common to both areas (Table 4). The number of species of graminoids, forbs and shrubs was higher on the mounds than on the intermounds. Sedges were recorded in only one station where they were found to be equally abundant on mounds and intermounds. More species of shrubs and graminoids were common to both areas than those unique to mounds and intermounds combined, but the species of forbs that were unique to both was higher than those that were common to both areas.

Of the 31 species of forbs on the mounds Alysicarpus rugosus, Corchorus tridentata, Oxygonum sinuatum, Schkurria pinnata and Senecio defacifolium occurred on most of them. No species of forbs occurring in the intermounds appeared in more than two stations. Of the 38 species of forbs common to both areas, Becium obovatum, Dyschoriste radicans, Gutenbergia cordifolia, Indigofera volkensisii, Pentanisia ouranogyne and Vigna schimperii were among the most abundant in all the six stations.

The seven graminoid species that were only recorded on mounds were mainly of the genera Aristida and Commelina. Those recorded only on the intermounds were of rare occurrence with most of them limited to a single sampling site. The dominant grass species common to both mounds and intermounds were Bothriochloa insculpta, Cymbopogon caseus, Cynodon dactylon, Digitaria scalarum, Pennisetum megianum and Themeda triandra.

Abuliton mauritianum and Lantana trifolia were among the shrubs unique to the mounds, while Grewia bicolor and G. tembensis were among those found only on intermounds. Shrubs common to both areas included Solanum incanum, Lippia javanica, Hibiscus aponeurus and Aspilia mosambicensis.

Table 4. Composition of plant species recorded on mounds and intermound areas. Data is obtained from six mound - intermound stations.

Growth Form	Spp. on Mounds only	Spp. on Intermounds only	Spp. Common to both Mounds and Intermounds	Total
Shrubs	6	2	12	20
Forbs	31	14	38	83
Graminoids	7	6	23	36
Sedges	0	0	2	2
TOTAL	44	22	75	141

Table 5. Comparison of plant species composition in the six mounds and intermound stations. The similarity in species composition is estimated using Jaccard's Community Coefficient.

Growth Form	Station	No. of species on mounds only	No. of species on Intermounds only	No. of species common to both areas	JCCI
Graminoids	1	4	2	12	66.7
	2	3	1	11	73.3
	3	8	7	7	31.8
	4	6	4	8	44.4
	5	4	0	10	71.4
	6	4	3	11	<u>61.1</u>
					$\bar{x} = 58.1 \pm 6.76 \text{ s.e.}$
Forbs	1	13	5	14	43.8
	2	10	11	15	41.7
	3	16	13	16	35.6
	4	10	7	15	46.9
	5	13	9	16	42.1
	6	11	2	10	<u>43.5</u>
					$\bar{x} = 42.3 \pm 1.53 \text{ s.e.}$
Shrubs	1	3	1	3	42.9
	2	2	3	4	44.4
	3	3	2	5	50.0
	4	3	4	4	36.4
	5	4	3	3	30.0
	6	4	1	3	<u>37.5</u>
					$\bar{x} = 40.2 \pm 2.87 \text{ s.e.}$

The only sedges recorded were Kyllinga leucocephala and Cyperus giolii. They were found only in one station where they showed wide distribution on both mounds and intermounds.

The degree of similarity in species composition between the two areas is highest in graminoids followed by forbs then shrubs (Table 5). The two areas were different in their forb and shrub composition, with significantly higher number of species of each category on the mounds, but were similar in their graminoid species.

There were three grass species that were significantly more frequent on the mounds, two on the intermounds and only one that showed random distribution (Table 6). Two species of forbs were more common on the mounds; five on the intermounds while one was evenly distributed. Among the shrubs, only Hibiscus aponeurus appeared in all six stations and was significantly more frequent on the mounds. Taken together, 13 out of 15 species showed non-random distribution with six of them being more frequent on the mounds and seven on the intermounds. All non-randomly distributed species showed a clear pattern with the number of runs (R) equal to two, which signified a distinct frequency demarcation along the median line (see Wonnacott and Wonnacott 1976).

The mean % cover for grass and forbs was higher on the intermounds (Table 7) while shrub cover was higher on the mounds. The differences, however, between the two habitats in each species category were not significant.

Mounds maintained significantly lower percent cover values than intermounds for the six preferred grass species (Table 7). When all grass species were considered together, no differences in cover were observed between mounds and intermounds but when taken individually, B. insculpta, C. dactylon and D. scalarum occurred more frequently on the mounds but none showed significant cover differences between the two areas. T. triandra and C. caseus, however, were the two grass species that occurred more frequently (Table 7) and maintained higher vegetation covers on the intermounds (Table 8). D. macroblephara had

Table 6. Frequency distribution of plant species that occurred on all six mounds and intermounds stations. A result of run's test. g = grass, h = herb, s = shrub. ($P < 0.05$, n.s. = not significant).

(i)	Species More Frequent on mounds	Median Frequency	Number of runs (r)	% occurrence		P
				Mound Top	One radius from Mound Edge	
	<u>Bothriochloa inculpta</u> (g)	30.5	2	66.7	50.0	0.034*
	<u>Cynodon dactylon</u> (g)	12.0	2	45.0	8.3	0.034*
	<u>Digitaria scalarum</u> (g)	15.0	2	50.0	16.7	0.034*
	<u>Pentanisia ouronygne</u> (h)	8.5	2	33.3	3.3	0.034*
	<u>Tagetes minuta</u> (h)	5.5	2	15.0	5.0	0.034*
	<u>Hibiscus aponeurus</u> (s)	13.0	2	40.0	20.0	0.034*
(ii)	<u>Species more Frequent on intermounds</u>					
	<u>Cymbopogon caseus</u> (g)	25.5	2	6.7	60.0	0.034*
	<u>Themeda triandra</u> (g)	33.0	2	33.3	56.6	0.034*
	<u>Vigna schimperii</u> (h)	9.0	2	3.3	25.0	0.034*
	<u>Becium obovatum</u> (h)					
	<u>Gutenbergia cordifolia</u> (s)	18.0	2	8.3	36.7	0.034*
	<u>Indigofera volkensii</u> (h)	19.0	2	16.7	38.3	0.034*
	<u>Tephrosia hildebrandtii</u> (s)	14.5	2	1.7	30.0	0.034*
(iii)	<u>Randomly Distributed Spp.</u>					
	<u>Digitaria macroblephara</u> (g)	14.0	3	11.7	21.7	0.212 n.s.
	<u>Dyschoriste radicans</u> (h)	2.5	4	0.0	6.7	0.500 n.s.

Table 7. Percent cover for grass, forbs and shrubs in the six mound and intermound stations. Comparison made using Anova. (P < 0.05, ns = not significant).

	Station	1	2	3	4	5	6	$\bar{x} \pm s.d.$	F(1,10)
Grasses	Mound	90.3	73.3	72.4	71.5	81.6	89.3	79.7 \pm 3.5	0.11 n.s.
	Intermound	95.5	71.5	59.5	84.4	88.8	92.8	81.9 \pm 5.6	
Forbs	Mound	21.6	22.6	13.1	10.2	20.1	10.8	16.3 \pm 2.2	1.17 n.s.
	Intermound	22.8	25.7	17.7	22.9	19.4	11.1	20.6 \pm 2.4	
Shrubs	Mound	2.5	13.0	18.5	25.3	12.0	2.8	12.5 \pm 3.6	0.23 n.s.
	Intermound	1.7	3.0	34.7	14.5	1.9	0.0	9.3 \pm 5.5	
<u>Most Preferred Grass Species</u>									
	Mound	68.5	40.8	28.3	35.7	39.8	60.7	45.65 \pm 6.35	4.94*
	Intermound	88.5	54.5	51.1	59.8	62.6	70.4	64.52 \pm 5.53	

Table 8. Mean percent cover for the most preferred grass species. Species means on mound and intermound stations are compared using t = test (P < 0.05, df = 10, n.s. = not significant).

Species		$\bar{x} \pm$ s.e.	n	
<u>Bothriochloa insculpta</u>				
Mound		12.1 \pm 4.4	6	2.00 n.s.
Intermound		11.3 \pm 4.0	6	
<u>Cymbopogon caseus</u>				
Mound		8.3 \pm 3.8	6	4.11*
Intermound		26.8 \pm 8.3	6	
<u>Cynodon dactylon</u>				
Mound		9.3 \pm 5.5	6	1.83 n.s.
Intermound		2.0 \pm 1.5	6	
<u>Digitaria macroblephara</u>				
Mound		3.2 \pm 1.1	6	1.00 n.s.
Intermound		4.2 \pm 4.1	6	
<u>Digitaria scalarum</u>				
Mound		7.7 \pm 3.8	6	1.65 n.s.
Intermound		3.4 \pm 1.2	6	
<u>Themeda triandra</u>				
Mound		8.4 \pm 2.5	6	3.07*
Intermound		16.7 \pm 5.2	6	

insignificant frequency and cover differences between the two areas (Table 8).

4.3.2 Net primary production, death and decomposition rates of mound and intermound vegetation

During the two rainy seasons, primary production was higher on mounds than on intermounds. The short rainy season mean(\pm s.d.) net primary production (NPP) was 691.9 ± 103.1 g/g live/day on the mounds and 460.6 ± 113.7 g/g live/day on intermounds. During this period, the mean NPP was 50% higher on mounds than intermounds and the difference was significant ($t = 21.63$, $df = 6$, $P < 0.05$).

The mean NPP during the long rainy season was 983.2 ± 47.1 and 840.1 ± 19.2 g/g live/day on the mounds and intermounds, respectively. The former were 17% more productive than the latter, a difference that was significant ($t = 3.19$, $df = 6$, $P < 0.05$).

The NPP was higher in both areas during the long rainy season than during the short one. Mounds were 42% more productive during the long rains than during the short rains whereas on the intermounds, the NPP values were 82% above those of the short rainy season. The mean difference in primary production between seasons was significant in each area ($t = 5.204$, $df = 6$, and $t = 4.018$, $df = 6$, $P < 0.05$ for the mounds and intermounds, respectively).

The long dry season, which lasted for five months, had a higher death rate of vegetation in both mounds and intermounds than the short dry season which lasted for three months. The long dry season mean death rate on the mounds was 17.2 ± 3.9 mg/g live/day and was significantly lower than the intermound mean of 36.9 ± 7.02 ($t = 6.242$, $df = 6$, $P < 0.05$). The mound vegetation mean death rate of 6.2 ± 1.9 mg/g live/day was significantly lower than that of the intermound vegetation of 13.5 ± 1.9 mg/g live/day during the short dry season that followed ($t = 90.4$, $df = 6$, $P < 0.001$). Seasonal death rate differences were evident in each of the two areas, with higher rates recorded in the long dry season ($t = 5.658$, $df = 6$, and $t = 4.522$, $df = 6$, $P < 0.05$ on mounds and

intermounds respectively). In each case, the death rate was about 170-180% higher during the long dry season. As the dry season progressed the intermound vegetation wilted and died out 3 to 4 weeks earlier than did the mound vegetation. The two areas exhibited no death rate during the rainy seasons.

Mean decomposition rate was 5.1 times higher on the mounds (7.6 ± 2.53 sd mg/g dead/day) than on the intermounds (1.5 ± 1.6 mg/g dead/day) during the long dry season ($df = (1, 6)$, $F = 16.57$, $n = 8$, $P < 0.01$). The mean decomposition rate was also higher on the mounds (5.0 ± 1.41 mg/g dead/day) than on the intermounds (3.8 ± 2.2 mg/g dead/day) during the short dry season but the difference was not significant.

Decomposition rates were strikingly similar between mounds and intermounds in each of the two annual wet seasons. Mean values were 3.5 ± 1.0 and 3.8 ± 1.61 mg/g dead/day on the mounds and intermounds respectively during the short rainy season, and 3.1 ± 0.7 and 3.1 ± 0.4 mg/g dead/day during the long wet season (fig. 2).

The decomposition rate on the intermounds appeared to be approximately constant throughout the year except during the long dry season when it fell to below half the value for the other three seasons. On the mounds, the rates seemed to be inversely affected by soil moisture levels as the highest rate was recorded in the driest season and the lowest in the wettest.

4.3.3 Crude protein content of mound and intermound vegetation.

All samples obtained from the mounds had higher mean protein content than those growing on the intermounds (Table 9).

Bothriochloa insculpta had higher mean crude protein values than Themeda triandra in both mounds and intermounds. T. triandra had significantly higher crude protein values in two mound stations than in the adjacent intermounds while insignificant differences were obtained between the two areas in the remaining two stations. Pooled data of T. triandra were 59% richer in mean

Figure 2: Mean decomposition rate of dead plant material in mound and intermound areas during the four annual seasons

Decomposition rate of vegetation in mg per gram dead per day

Mounds
 intermounds

NB: The bars in this and subsequent figures represent standard errors

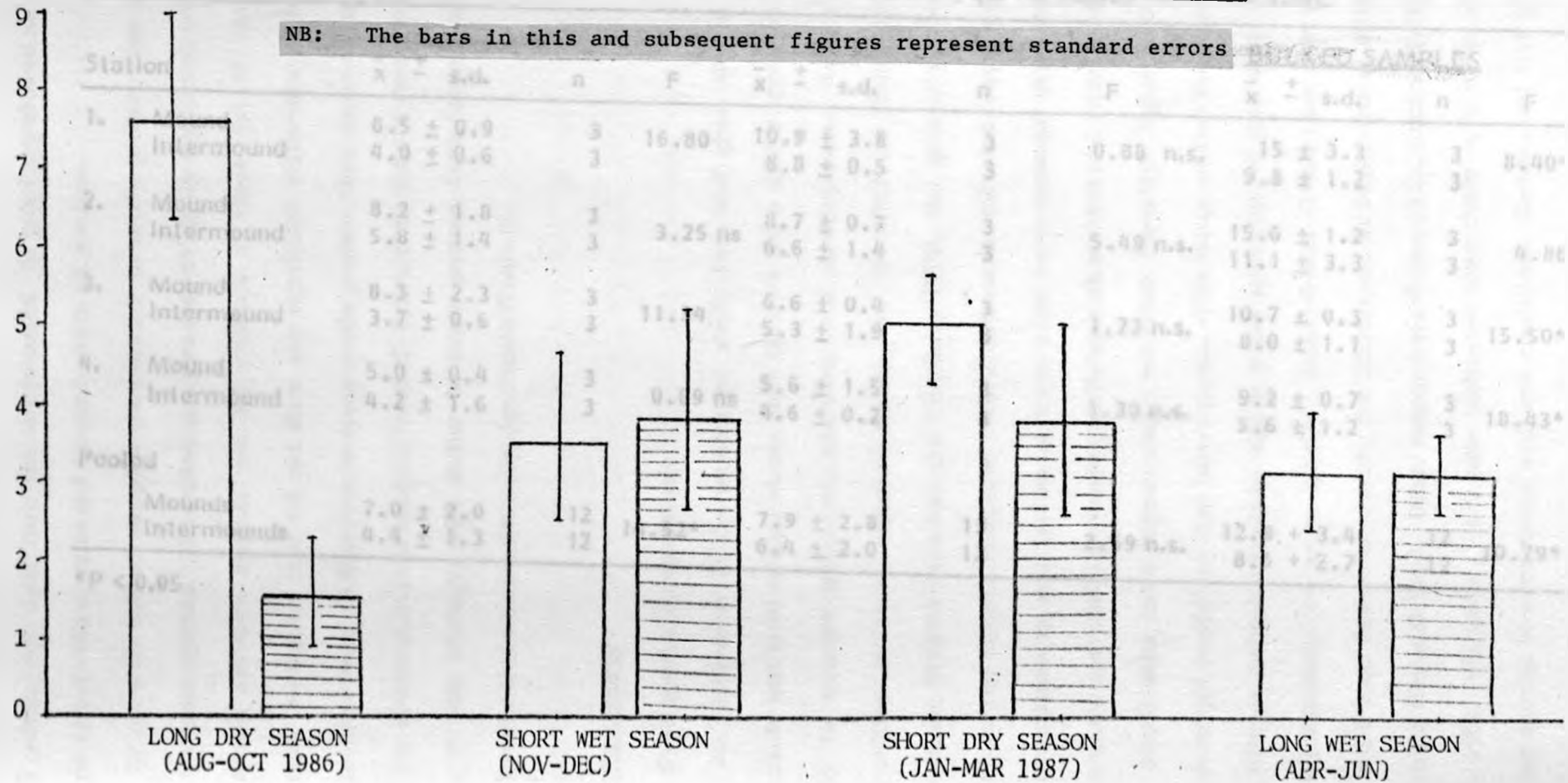


Table 9. Comparison of the crude protein of two important grass species and bulked vegetation samples obtained from mounds and intermounds. DF = (1,4) in each of the four stations and (1, 22) for pooled data. P < 0.05).

Station	<u>THEMEDA TRIANDRA</u>					<u>BOTIRIOCHLOA INSCULPTA</u>					<u>BULKED SAMPLES</u>					
	\bar{x}	\pm	s.d.	n	F	\bar{x}	\pm	s.d.	n	F	\bar{x}	\pm	s.d.	n	F	
1.	Mound	6.5	\pm	0.9	3	16.80	10.9	\pm	3.8	3	0.88 n.s.	15	\pm	3.3	3	8.40*
	Intermound	4.0	\pm	0.6	3		8.8	\pm	0.5	3		9.8	\pm	1.2	3	
2.	Mound	8.2	\pm	1.8	3	3.25 ns	8.7	\pm	0.7	3	5.49 n.s.	15.6	\pm	1.2	3	4.88 n.s.
	Intermound	5.8	\pm	1.4	3		6.6	\pm	1.4	3		11.1	\pm	3.3	3	
3.	Mound	8.3	\pm	2.3	3	11.34	6.6	\pm	0.4	3	1.23 n.s.	10.7	\pm	0.3	3	15.50*
	Intermound	3.7	\pm	0.6	3		5.3	\pm	1.9	3		8.0	\pm	1.1	3	
4.	Mound	5.0	\pm	0.4	3	0.69 ns	5.6	\pm	1.5	3	1.30 n.s.	9.2	\pm	0.7	3	18.43*
	Intermound	4.2	\pm	1.6	3		4.6	\pm	0.2	3		5.6	\pm	1.2	3	
Pooled																
	Mounds	7.0	\pm	2.0	12	14.52*	7.9	\pm	2.8	13	2.59 n.s.	12.8	\pm	3.4	12	10.79*
	Intermounds	4.4	\pm	1.3	12		6.4	\pm	2.0	12		8.6	\pm	2.7	12	

*P < 0.05

crude protein than data from the intermounds. B. insculpta showed no significant difference between mounds and intermounds in all stations.

In general, bulked samples were richer in crude protein than samples of the two grass species. The bulked samples showed highly significant crude protein differences between mounds and intermounds in three out of four stations. However, the station that did not show any significant difference did have mound samples that were 41% richer in mean crude protein than those on intermounds. Data for combined bulked samples from all the stations showed that mound samples were, on the average, 49% richer in crude protein than intermound samples, a difference that was statistically significant (Table 9).

4.4 DISCUSSION

4.4.1 Plant species composition

The difference in the number of shrub, forb and grass species supported by mounds and intermounds shows that the two areas differ appreciably in their ability to enhance plant establishment and development. Although no two communities or even adjacent stands are identical in their plant species composition (Mueller-Dombois and Ellenberg 1974), the greater number of plant species on the mounds compared with intermounds indicates that the differences are in response to soil factors as most other environmental attributes (such as temperature and rainfall) operate equally on both mounds and intermounds.

Mound soils have higher water retention capacity, higher nutrient levels and better pH conditions than intermounds. This indicates that the mounds provide a significant habitat variation with a wider spectrum of conditions that favour the establishment of more species. Heritz-Smith (1962) has also singled out soil as the main factor accounting for differences in vegetation in different parts of Nairobi National Park. Other researchers (Olsen 1923, Stalfelt 1972, Ellenberg 1950, 1952, Whittaker 1967) have indicated that there is a varied distribution of plant species in accordance with soil conditions. Gakahu and Cox (1984) found

more species on mounds than on intermounds near Nyahururu, Kenya while Cox and Zedler (1986) obtained similar results in the mounded terrain of Tijuana Estuary, Texas. Authors of both studies attributed their observations to differences in mound and intermound soils. Del Moral and Deardorff (1976) found the same vegetation trend in the Mima mounds of Washington State, U.S.A. and gave the same explanation.

Factors such as grazing and trampling, which are known to bring about floristic variation between two areas (Pratt and Gwynne 1977, McNaughton 1976), are higher on the mounds than on the intermounds as is illustrated later in this study and pointed out by other researchers (Lusigi 1977, Scott 1963, Gakahu and Cox 1984). When the mound soils which are capable of supporting more plant species are further stimulated by grazing and browsing, the difference between the mounds and intermounds in terms of their species composition would be expected to be even more pronounced.

Differences in the number of plant species found on mounds versus intermounds is of significance to grazing animals as most herbivores in the Park are known to be selective feeders (Gakahu 1982, Field 1968, Lamprey, 1963, Stewart and Stewart 1970, Gwynne and Bell 1968, Estes 1967). The greater number of plant species on the mounds would influence their feeding strategies with greater preference given to the mound vegetation due to its wider range of food items.

The distribution of most plant species that occurred in both habitats displayed a non-random pattern with some species increasing and others decreasing in frequency from the mounds to the intermounds. This kind of distribution may be an important factor in determining the amount of food resources available to, and utilized by herbivores since it implies differences in abundance between the two areas. As most of the important grass species preferred by herbivores occurred more frequently on the mounds, more animals would be expected to show preference for feeding on them.

Some factors other than soils and grazing intensity that make species distribution analysis difficult to establish through field observations include plant to plant interactions, trampling by animals, waste matter deposition, fresh mole rat heaps on intermounds and active burrowing on the mounds by warthogs. These factors may have obscured the relationships between species distribution and factors examined in this study.

The cover of shrubs and forbs and their abundance showed striking contrasts between mounds and intermounds. Although the species of each category were more abundant on the mounds, their cover was equal in the two areas contrary to expectation. This contrast may have been caused by higher utilization of mounded grasslands by herbivores, which would reduce cover where intensity was highest. Cox and Gakahu (1985) observed a similar vegetation cover reduction on mounds near Jomo Kenyatta International Airport, a few kilometers north of the present study site and at another site near Kenyatta University, Nairobi. They attributed the observations to higher grazing on the mounds.

The assumption that each species should have higher percent cover in the habitat it occurred most frequently did not hold true for most grass species of recognised grazing value. B. insculpta, C. dactylon, and D. scalarum which were significantly more frequent on the mounds had insignificant cover differences between the two areas. Themeda triandra and Cymbopogon caseus were more frequent and maintained higher cover values on the intermounds. That the species occurring on mounds were more heavily grazed suggests that there may be differences in the palatability levels between mound and intermound vegetation. Lusigi (1977) and Scott (1963) observed heavier grazing on the same mounds and suggested that grasses on mounds seemed more palatable to grazers than the grass growing between them.

Shrub cover was higher on the mounds than on the intermounds. This was not surprising as there were 29% more shrub species on the mounds whereas there were few browsing animal species recorded feeding in the area. Cox and

Gakahu (1985) also found higher shrub cover on the mounds.

4.4.2 Net primary production, death and decomposition rates of mound and intermound vegetation

The difference in net primary production (NPP) between mounds and intermounds suggests that the role of mound-building animals is important in the ecology of mounded grasslands. NPP results follow the soil textural and mineralogical status which were found to be more favourable for plant growth on the mounds.

Assuming that the environmental factors that affect plant growth such as light, temperature and water were constant and that other extraneous factors such as grazing, trampling and dung deposition were controlled by use of exclosures, differences in NPP between mounds and intermounds may have been in response to differences in their soil fertility status. Although the water-retention capacity of the mound and intermound soils is different and the former have better drainage due to their general elevation, soil-water differences between the two areas were assumed to be of no consequence as the NPP measurements were taken during the rainy season growth periods when water was not a limiting factor.

Mounds in Nairobi National Park were 15 - 50% more productive than intermounds but probably even higher values could have been recorded if the mounds were exclosed from animal use for a period long enough to allow strong establishment of vegetation most of which was heavily grazed during the preceding dry seasons. Cook (1971) has shown that grazing intensity may affect the vigour of vegetation regrowth in both directions depending upon the level of defoliation.

The role of rainfall in determining NPP was particularly marked. NPP was less during the short rains than during the long rains in both mounds and intermounds. It appears, therefore, that NPP is positively correlated with the

amount and duration of rainfall but limited by soil nutrient availability. Walter (1954), and Strugnell and Pigott (1978) have also shown a direct relationship between water availability and above ground NPP in tropical and savanna grasslands respectively. Deshmukh (1986) found the NPP of the grasslands 5 km west of the present study site to be 55% higher during the long rains than during the short ones. He recorded 420 g/m² and 651 g/m² during the short and long rains respectively, figures that were slightly lower than those reported here by 9.5% and 29% during the same seasons. The differences may be due to variations in weather conditions and/or site specific soil conditions. The findings of this study are closer to the estimated annual average of 890 g/m² for savanna grasslands (Lieth and Whittaker 1975).

Studies within the neighbouring grasslands provide further evidence that mounds are more productive than intermounds. Fairburn (1963) recorded more vegetation production on the Thika mounds while Scott (1963) and Stephen et al. (1956) commented on the higher primary production on the mounds on the Athi-Kapiti grassland. In U.S.A., Allgood and Grey (1974) in Oklahoma, Branson et al. (1965) and McGinnies (1960) in Colorado, found plant productivity on mounds to be from 32 to over 200% higher than on intermounds.

The higher death rate of intermound vegetation during the dry season may be attributed to its poor soil nutrient status and inability to retain moisture for as long as mound soils. The lower clay and silt content in intermound soils reduce moisture retention capacity, and the higher sand and gravel content allow fast water percolation and raise soil temperature (Russell 1973), results which would cause faster drying up of intermound soils. This contention is supported by the drying up of intermound vegetation about four weeks before mound vegetation. The death rate of vegetation in each habitat during the long dry season was three times above the rates recorded during the short dry season. Vegetation death rate appears to be closely related to changing soil-moisture conditions. The zero death rate observed during the wet seasons suggests that growth rate was

higher than death rate.

The decomposition of organic matter, a process carried out by soil micro-organisms would be expected to be determined by factors that favour the occupation of the soils by micro-organisms. Soil aeration, moisture, temperature and pH determine the chemical and physical environment that determines microbial activity. As the micro-organisms derive their energy requirements from this process, they would be expected to be more active in areas that provide higher levels of organic matter.

Mound soils have higher clay levels than those of the intermounds. Clay is a soil constituent that has the highest water retention capacity and which becomes cold during the wet season (Russell 1973). During the wet seasons, microbial activity on the mounds may have been lowered by low soil temperatures and reduced aeration due to micropore saturation. The removal of these factors during the dry season may have raised microbial activity and consequently, led to higher decomposition rates. On intermounds, the decomposition rate did not appear to be affected by the wetting of the soil, probably due to the low silt and clay levels. Decomposition rates on the intermound, however, were probably reduced by lower moisture levels during the long dry season as their soils appear to be more prone to water loss.

Micro-organisms mainly prefer nearly neutral soils (Jarvis and Jarvis, 1972, Russell 1973). Intermounds, with their acidic soils create a less favourable environment for the micro-organisms than the mounds whose pH is nearly neutral. The mounds could also maintain more micro-organisms as they produce vegetation of higher nutrient status (see results on % crude protein) than do intermounds.

Soil calcium levels are higher on mound soils than on intermound soils. Soils with good supply of calcium favour higher decomposition (Thomson and Troeh 1979), a factor that helps explain the observed higher decomposition rates on mounds. Cox (personal communication) suggests that the lower decomposition rate is caused by the intermound plants being of poorer nutrient quality. Thomson

and Troeh (1979) proposed that the energy obtained by micro-organisms from dead plant residues is one of the most important factors affecting their activity and is frequently a limiting factor in rates of decomposition.

The higher decomposition rate on the mounds observed during the dry seasons should improve nutrient cycling, by releasing more nutrients into the soil and making them available to the plants during the rainy season that follows. Lower decomposition on the intermounds may mean less efficient nutrient cycling.

4.4.3 Crude protein of mound and intermound vegetation.

Bothriochloa insculpta, which is commonly known as the sweet pitted grass, occurs in scattered grasslands, and is usually associated with Themeda triandra. It is reportedly a very palatable grass capable of rapid recovery even after heavy grazing. T. triandra (red oat grass) is equally valuable in grazing pasture, best suited to light grazing under dry conditions and rapidly disappears under intensive grazing (Edward and Bogdan, 1951).

The bulked samples were of different grazing value. Some genera like those of Commelina, Vigna, Dolichos, Sericocomopsis, Cynodon and Digitaria are of great pasture value while others like Pennisetum, Eragrostis, Tephrosia, Rhynchosia, Solanum, Lippia and Ocimum are undesirable to most grazing herbivores (Edwards and Bogdan 1951).

There was a consistent trend of higher crude protein content in the plants growing on the mounds than those growing on the intermounds. It seems anomalous that plants growing in the two areas should differ in their crude protein content as the areas have the same levels of total nitrogen in their soils. A factor or factors that enhance greater absorption of nitrogen from mound soils must exist to explain this difference. Calcium, which increases ion uptake by plants (Jarvis and Jarvis 1972), was higher on mounds than on intermounds. Low soil pH considerably reduces microbial activity and available nitrogen is subsequently lowered, regardless of total nitrogen level (Landon 1984). The intermound soils

support plant that probably suffer the double disadvantage of having to grow in soils with a poorer ability to absorb nitrogen and with lower available nitrogen due to increased acidity. Crude protein of grasses and legumes is directly affected by soil chemical conditions, especially pH which limits nitrogen availability (Lyttleton 1973).

Most of the grass samples obtained from intermounds fell below the 6% crude protein level, below which the appetite of grazing animals is depressed (Minson 1976). Most of the grass samples obtained from mounds were above this level.

Higher protein content in plant species growing on mounds supports the hypothesis that herbivores would be expected to spend more time feeding on the mounds and consequently removing more vegetation. As protein is the major nutrient that limits large herbivore grazers in the East African savannas (Sinclair 1975), the selection of plants with higher crude protein should be an important aspect in the feeding strategies of large grazing herbivores.

CHAPTER 5

HABITAT PREFERENCE AND GRAZING HARVEST

5.1 INTRODUCTION

This section investigates herbivore grazing activity to establish the seasonal interactions between vegetation and herbivores in the mounded grasslands. The observations that mounds in Nairobi National Park are more heavily grazed than the adjacent intermounds (Cox and Gakahu 1985) is evaluated by measuring the actual vegetation grazed in each annual season

5.2 METHODS

5.2.1 Habitat preference

Preliminary surveys to establish a transect route along a representative section of the mounded grassland were carried out in July and August 1986 in Nairobi National Park. The Middle Ridge area was found to have the most extensive and well developed mounds in the Park. A permanent road transect 6 km long and 300 m wide was established in this area traversing areas of well established and conspicuously defined mounded habitats. The specific location of the transect was determined by accessibility by vehicle, ease of sighting animals and accuracy of documenting their activities.

The number of individuals of each species of large grazing herbivores feeding in each area was recorded once every week between 6.30 a.m. and 8.30 a.m. along the established route. The observations were made for a set period of five minutes on every individual or herds of herbivores sighted.

The area covered by each mound was estimated by measuring its diameter and using the formula for the area of an ellipse and an estimate of the percent area covered by mounds and intermounds was calculated. The data on the location of all the feeding animals were compared. The observations for each animal species feeding on mounds and intermounds were also compared for each season.

5.1.2 Grazing harvest

Grazing harvest was estimated by comparing the weight of vegetation in replicate 0.1 m² plots inside and outside enclosures at the beginning and end of every season. The specific methods were described together with those for determining net primary production.

The total grazed live tissue, G, was calculated using the formula:

$$G = b + p - d - g. \text{ (Cox and Waithaka, in press)}$$

where:

G = amount of vegetation grazed in g/0.1 m plot

b = weight of live tissue at the beginning of the season

p = NPP during the season

d = Mortality of live tissue during the season

g = wt of live tissue at the end of the season.

The amount of vegetation grazed from mounds and intermounds was compared for every season.

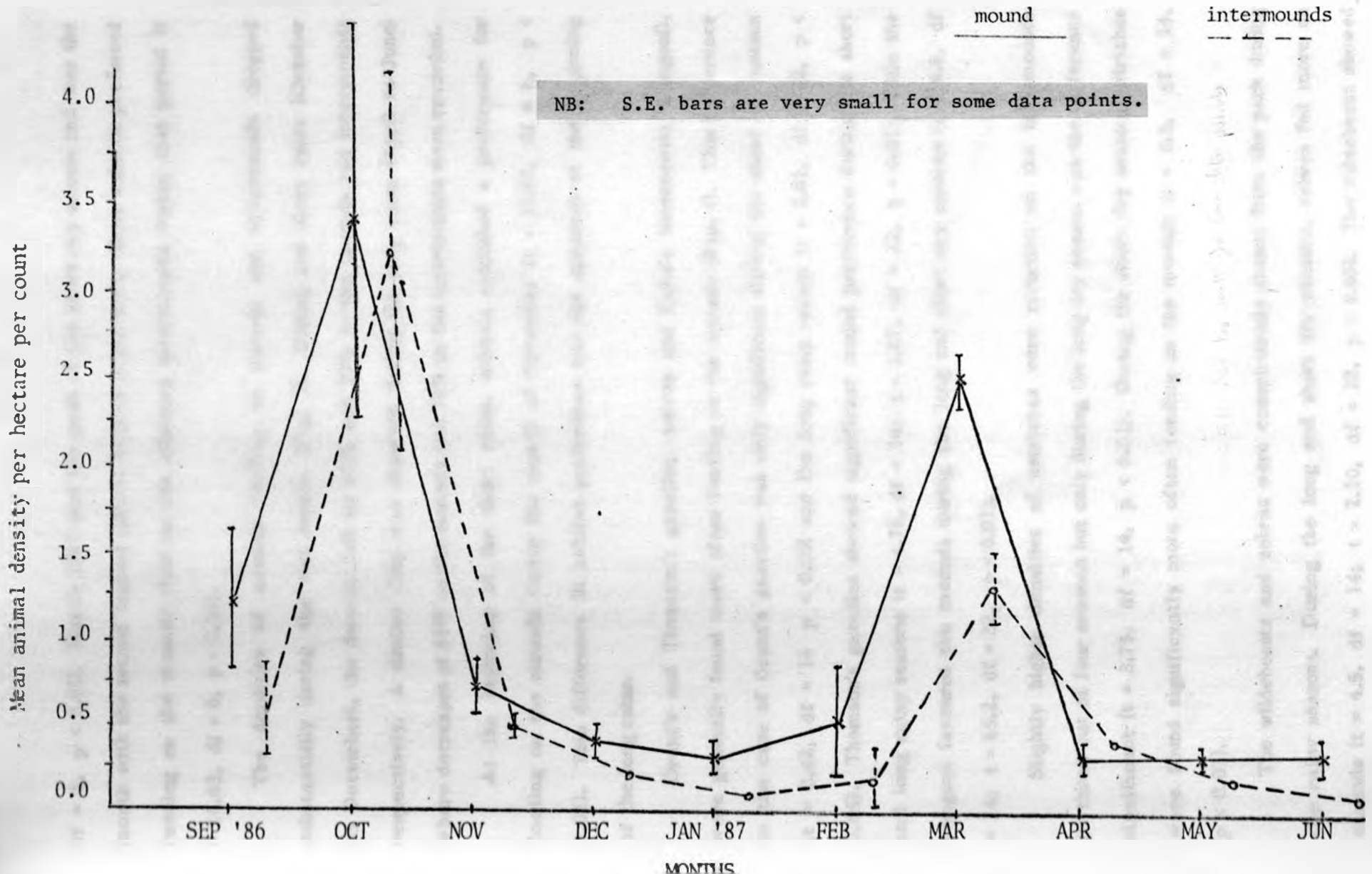
5.3 RESULTS

5.3.1 Habitat preference

Mounds covered approximately 19% of the total transect area of 180 ha. Low animal densities of less than one animal/ha were recorded in eight out of the ten months that counts were done (Fig. 3). The months of October 1986 and March 1987 were the only periods when mean animal densities were in excess of one animal/ha in each of the two habitats. Consistently higher animal densities were recorded feeding on the mounds than on the intermounds during the period of study except for April 1987 when the two areas had approximately equal animal densities.

The highest density of animals feeding on the mound-intermound areas was in October 1986 which corresponded with the peak of the long dry season. Animals during this period showed no difference in habitat preference ($t = 0.63$,

Figure 3: Differences in mound and intermound food resources utilization by herbivores



df = 6, $p < 0.05$). March 1987 was the peak of the short dry season and was the month with the second highest animal density in the area. More animals preferred feeding on the mounds than on the adjacent intermounds during that period ($t = 16.63$, $df = 6$, $p < 0.01$).

The densities of animals feeding on mounds and intermounds dropped substantially during the wet season (Fig. 3). During the short rains (October to December), the density fell by 86% and 93% in the mounds and intermounds respectively. A similar drop was observed during the long rains (April to June) where decreases of 89% on the mounds and 79% on the intermounds were recorded.

At the beginning of the short rains, animals exhibited a preference for feeding on the mounds during the month of November ($t = 31.91$, $df = 6$, $p < 0.01$). This difference in habitat preference was not apparent at the beginning of the long rains.

Grant's and Thomson's gazelles, zebras and Coke's hartebeests (kongoni), were generally found more often feeding on the mounds (Fig. 4). This preference in the case of Grant's gazelles was only significant during the short dry season ($t = 2.42$, $df = 14$, $p < 0.05$) and the long rainy season ($t = 2.61$, $df = 22$, $p < 0.05$). Thomson's gazelles showed significant mound preference during the short and long rainy seasons ($t = 4.78$, $df = 14$; $t = 3.67$, $df = 22$, $p < 0.01$), while the kongoni favoured the mounds during the long and short dry seasons ($t = 4.8$, $df = 14$; $t = 65.2$, $df = 22$, $p < 0.01$).

Slightly higher densities of ostriches were recorded on the intermounds in three out of four seasons but only during the long dry season was the difference significant ($t = 3.75$, $df = 14$, $p < 0.01$). During the short dry season, ostriches were found significantly more often feeding on the mounds ($t = 8.5$, $df = 14$, $p < 0.01$).

The wildebeests and zebras were conspicuously absent from the park during the rainy seasons. During the long and short dry seasons, zebras fed more on mounds ($t = 4.5$, $df = 14$; $t = 2.10$, $df = 22$, $p < 0.05$). The wildebeest showed

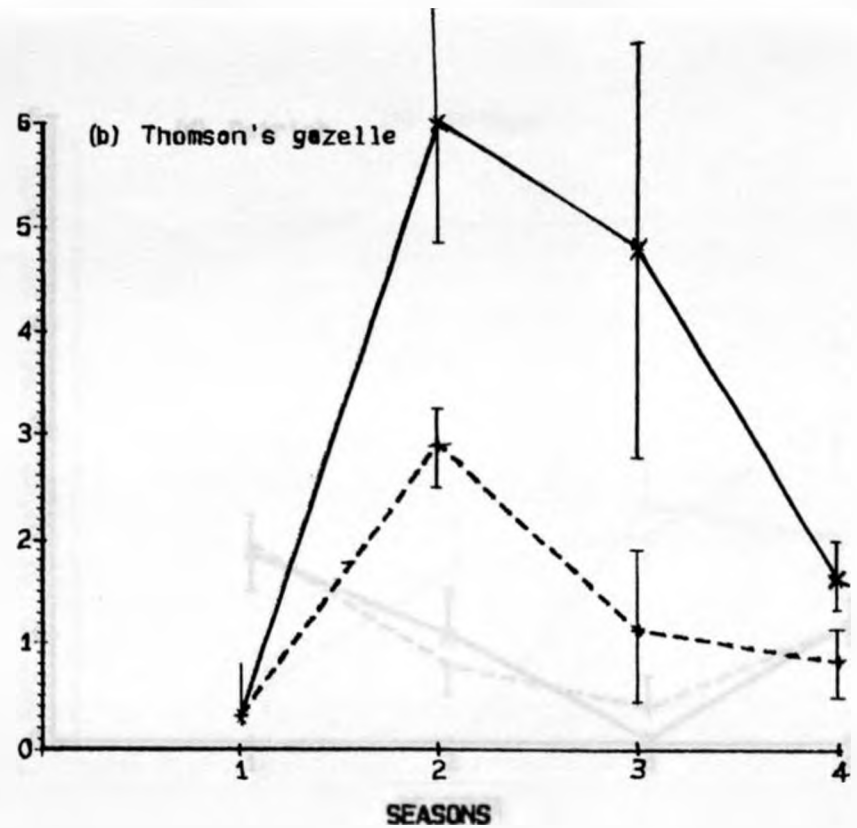
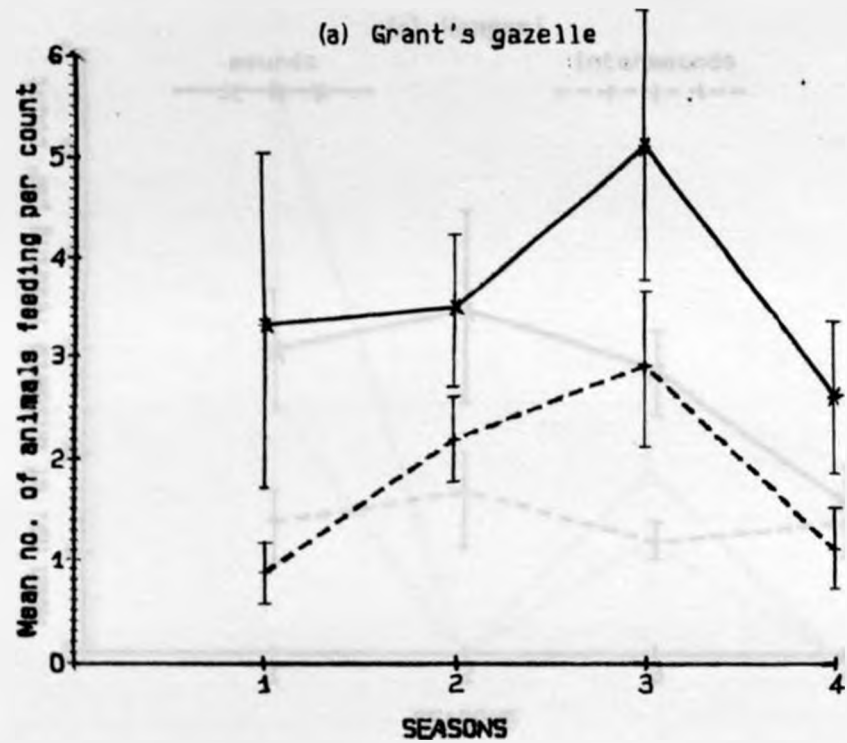
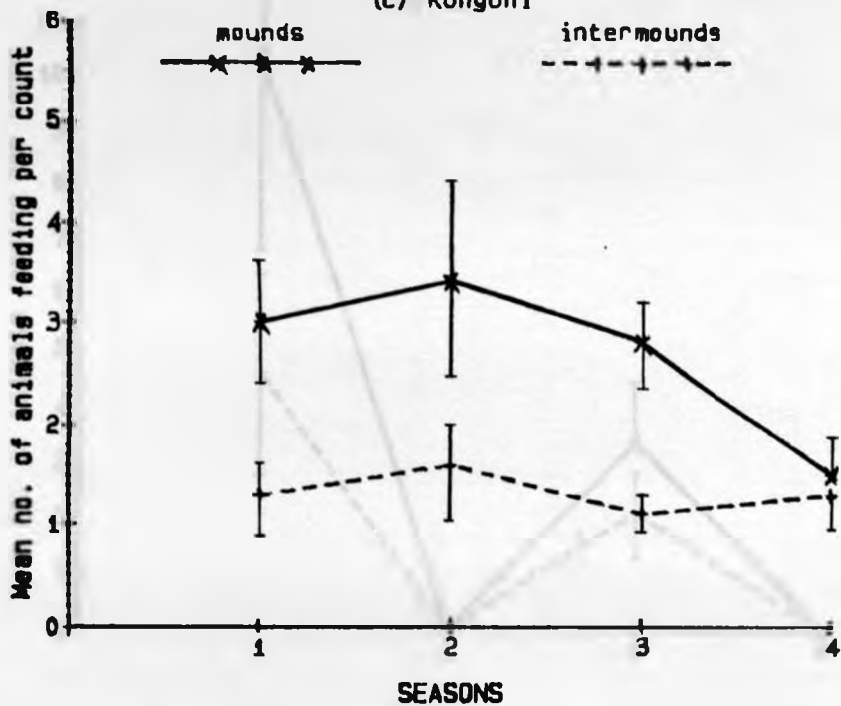
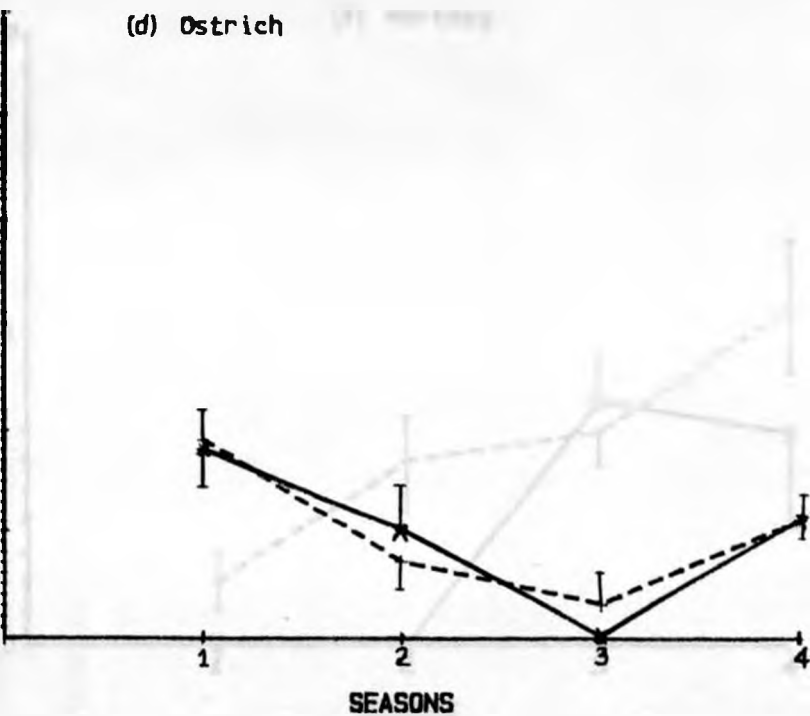


Figure 4. Feeding distribution of Grant's gazelle (a), Thomson's gazelle (b), Kongoni (c), Ostrich (d), Zebra (e), Warthog (f) and Wildebeest (g) within the mound and intermound areas . Long dry season = 1, short rainy season = 2, short dry season = 3, long rainy season = 4. **Eight counts were** made during seasons 1 and 2 and twelve counts during seasons 3 and 4.

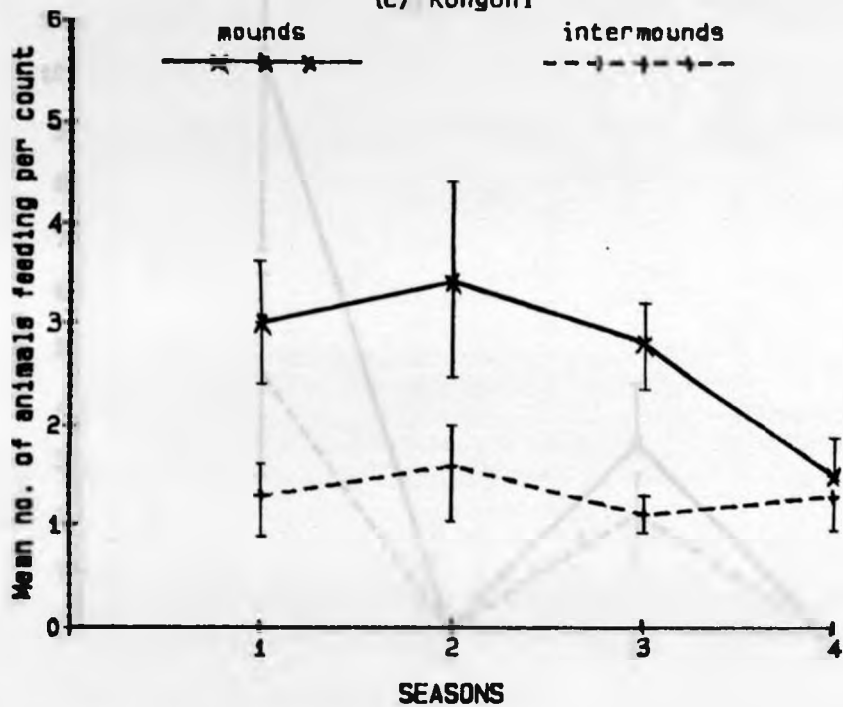
(c) Kongoni



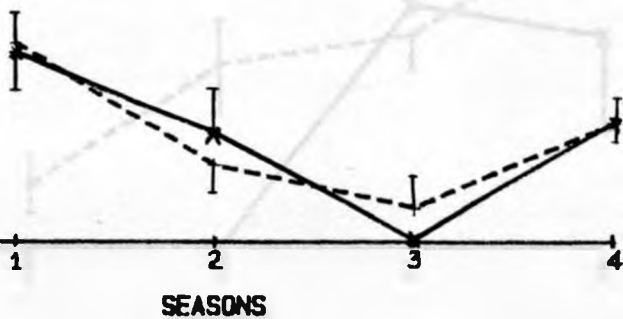
(d) Ostrich



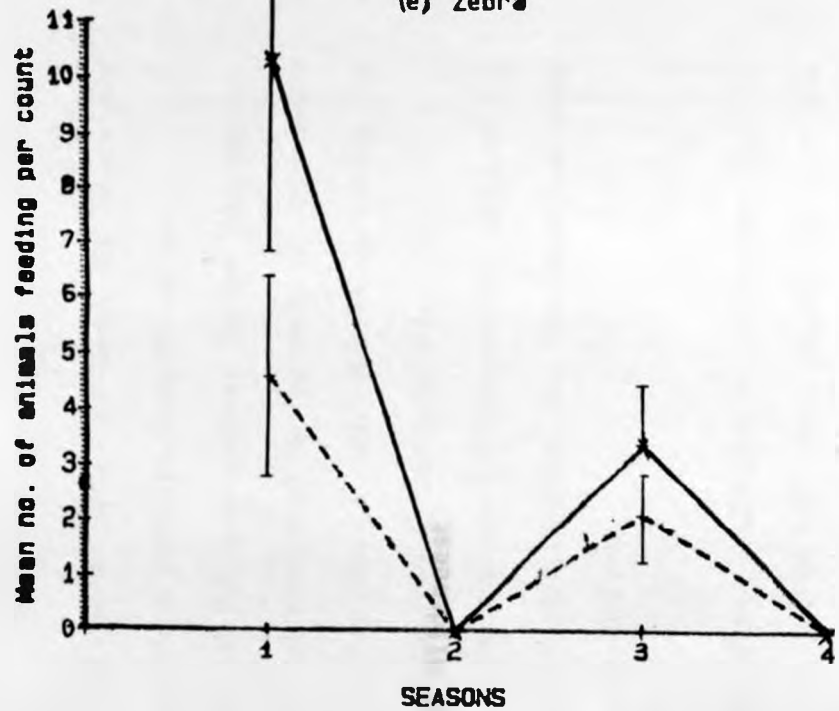
(c) Kongoni



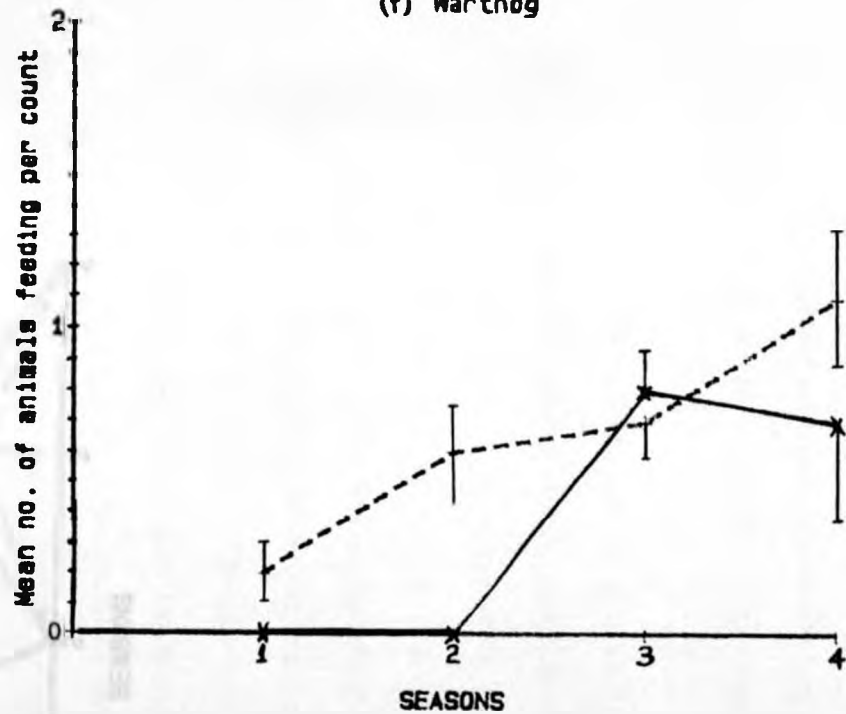
(d) Ostrich



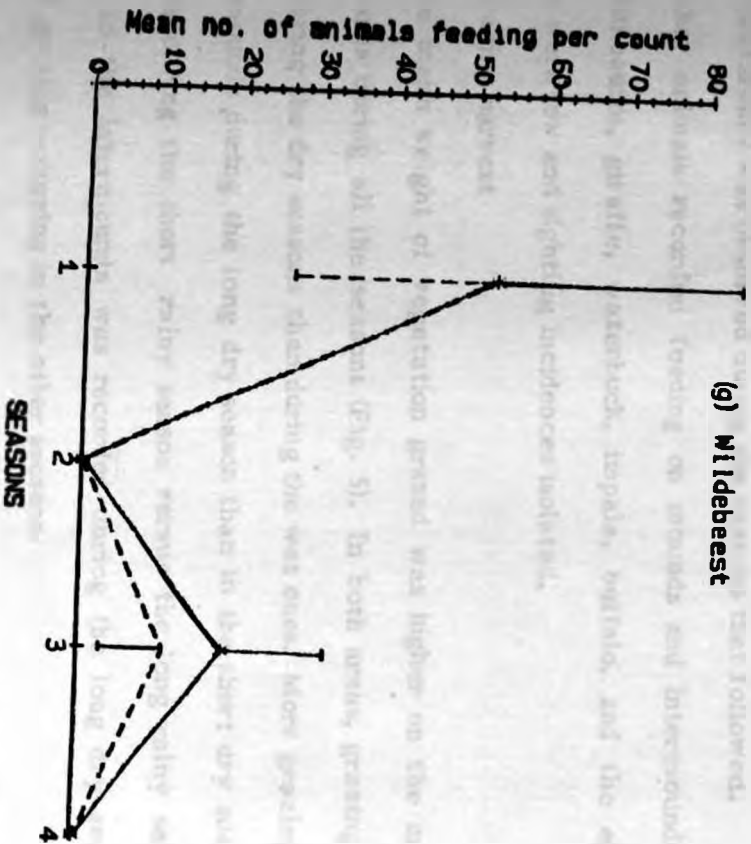
(e) Zebra



(f) Warthog



(g) Wildebeest



higher but non-significant mound preference during the short dry season and equal preference for mounds and intermounds during the long dry season.

Warthogs were recorded during all the four seasons. In the long dry and short rainy seasons, none were recorded feeding on the mounds, and intermound preference was significant ($t = 2.86$, $df = 14$; $t = 2.22$, $df = 14$, $p < 0.05$). No habitat preference was observed during the seasons that followed.

Other animals recorded feeding on mounds and intermounds included the black rhinoceros, giraffe, waterbuck, impala, buffalo, and the eland but their numbers were low and sighting incidences isolated.

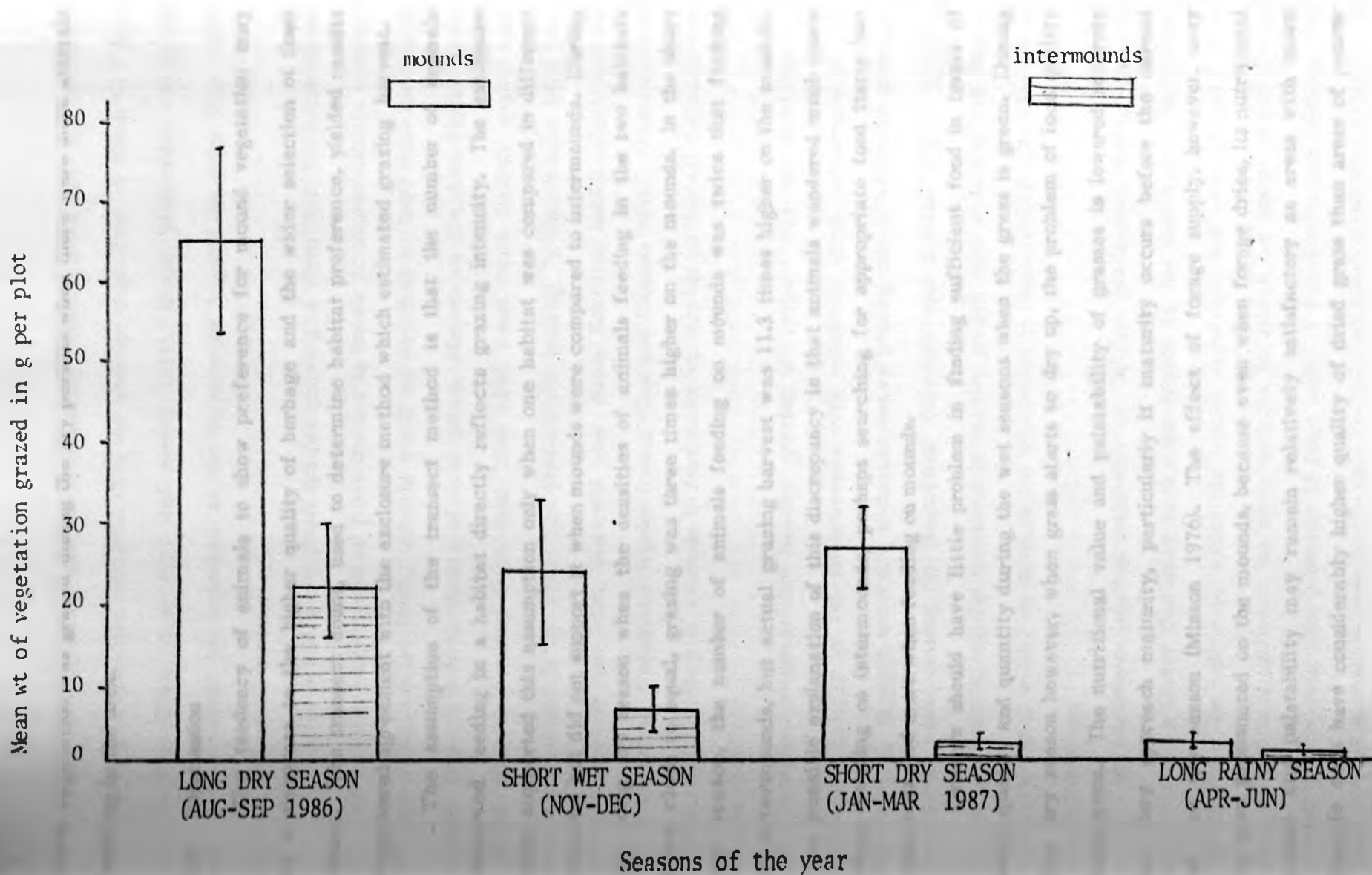
5.3.2 Grazing harvest

The mean weight of vegetation grazed was higher on the mounds than on intermounds during all the seasons (Fig. 5). In both areas, grazing intensity was higher during the dry seasons than during the wet ones. More grazing was recorded on the mounds during the long dry season than in the short dry season. This was also true during the short rainy season versus the long rainy season. Highest grazing in the intermounds was recorded during the long dry season with low levels of grazing occurring in the other seasons.

Harvest by grazing during the long dry season was 653.7 g/m^2 and 240 g/m^2 on the mounds and intermounds respectively. These values corresponded to approximately 66% and 29% of the total net primary production on the mounds and intermounds respectively during the previous long rainy season. This difference was significant ($t = 6.35$, $df = 6$, $p < 0.01$). During the short dry season, corresponding weights of the grazed vegetation were 39% and 5% of the net primary production of the preceeding short rainy season on the mounds and intermounds respectively. This difference was also significant ($t = 7.32$, $df = 6$, $p < 0.01$)

The weights of vegetation harvested by grazing during both wet seasons were not significant at $p < 0.05$. The number of animals recorded in the area and the weight of vegetation grazed showed a wet-dry season cyclic pattern.

Figure 5: Difference in grazing intensity between mounds and intermounds in different season



More vegetation was grazed during the dry periods when there were more animals feeding in the area.

5.4 Discussion

The tendency of animals to show preference for mound vegetation may be a response to the higher quality of herbage and the wider selection of food items. The transect count, used to determine habitat preference, yielded results in general agreement with the enclosure method which estimated grazing harvest.

The assumption of the transect method is that the number of animals observed feeding in a habitat directly reflects grazing intensity. The enclosure data supported this assumption only when one habitat was compared in different seasons but did not support it when mounds were compared to intermounds. During the long dry season when the densities of animals feeding in the two habitats were close to equal, grazing was three times higher on the mounds. In the short dry season, the number of animals feeding on mounds was twice that feeding on intermounds, but actual grazing harvest was 11.3 times higher on the mounds. One possible explanation of this discrepancy is that animals wandered much more when feeding on intermounds, perhaps searching for appropriate food items but concentrated more when feeding on mounds.

Grazers should have little problem in finding sufficient food in terms of both quality and quantity during the wet seasons when the grass is green. During the dry season however, when grass starts to dry up, the problem of food quality increases. The nutritional value and palatability of grasses is lowered severely as they approach maturity, particularly if maturity occurs before the advent of the dry season (Minson 1976). The effect of forage supply, however, may be less pronounced on the mounds, because even when forage dries, its nutritional value and palatability may remain relatively satisfactory as areas with more fertile soils have considerably higher quality of dried grass than areas of poorer soils (Peterson 1967).

The diet of grazing animals consistently contains more leaf and less stem, more live and less dead material than the average vegetation to which they have access (Van Dyne et al 1980 and Arnold 1981). Mound preference during the dry season would be expected as the intermound vegetation dries four weeks before that on intermounds.

The mounds had more plant species growing on them than the intermounds. As the relative proportions of plant species is known to affect habitat selection (Koegh 1973, Hunter 1962), animals would be expected to feed more on mounds where there is a wide choice of food items. Mounds on the Athi Plains (within which Nairobi National Park lies) have been found more heavily grazed than the intermounds (Scott 1963) and preferential grazing by mammalian herbivores on the mounds has been observed near Jomo Kenyatta International Airport, Nairobi and at Waunyumu Ngeke Ranch (Cox and Gakahu 1985). Another study reported a tendency of animals to feed more on mounds in Nairobi National Park (Lusigi 1977).

Indirect evidence for heavier grazing on mounds was the dominance of Themeda triandra in the intermounds with relatively lower occurrence in the mounds. T. triandra does not withstand heavy grazing and is known to gradually disappear when grazing is intensified (Edwards and Bogdan 1951). Cynodon dactylon, which is usually dominant in heavily grazed sites (Edwards and Bogdan 1951) occurred widely on mounds but was found at considerably lower frequency in intermounds.

The herbivores studied exhibited no habitat preference during the long dry season, a factor that may have been caused by the depletion of the mound resources. The extent to which the mound vegetation had been grazed late in that season was sufficient to force animals to search for lower quality forage in the intermounds. The presence of large herds of wildebeests and zebras during that season may have been the main cause of vegetation depletion which would have a direct effect of reducing the number of other herbivores feeding in the

area. These animals reduced the vegetation on the mounds into forage probably unacceptable to the fine grazers like the Thomson's gazelle. In the following short dry season, fewer zebras and wildebeests were recorded feeding in this area and consequently the degree of defoliation was less intense. More Thomson's and Grant's gazelles were found feeding in the area.

During the rainy seasons, ample food was available within the two areas but animals continued to show preference for mound vegetation. The gazelles and hartebeests fed more intensively on the proliferating shoots emerging from the previously overgrazed mounds. This was most evident after the onset of the short rains which were preceded by very severe grazing.

Defoliation by grazing has been reported to stimulate growth (Wareing et al 1968, Hodgkinson 1974, Dyer and Bakhari 1976, Cadwell et al. 1981, McNaughton 1979, 1983, 1985) and recycling of nutrients (Chew 1974, Mattson and Addy 1975, Batzli 1978), and to be important in stimulating productivity (McNaughton 1979, Cargill and Jefferies 1984). Defoliation brings about a great number of quickly growing tillers of higher photosynthetic capacity and greater flexibility of resource allocation (Cadwell et al. 1981). These compensatory growth responses are strongly regulated by nutrient supply (Wallace et al 1982). This implies that vegetation on the mounds grows faster when rain falls because of the heavier dry season grazing and better nutrient supply.

The grazing of tall grass by wildebeests and zebras stimulated growth by forcing the grass to tiller and so produce a short, dense mat of green grass suitable for Thomson's gazelle. Wildebeests, zebras and Thomson's gazelles eat the same species of plants but at different stages of growth (Estes 1967). This pattern was evident when the short rains started but was less marked after the onset of the long rains probably because the less severe defoliation of the previous short dry season was insufficient to cause rapid compensatory growth on the mounds. As a result, the animals foraged widely in the park as food was superabundant.

Defoliation by grazing of 75% is considered too severe (Cook 1971). However, the data available show that between 36% and 88% of the vegetation in the mounds was harvested by grazing. This ranks them with the most intensively grazed grasslands in the world.

5.1. Theoretical considerations concerning mounds and burrows.

The mounds could generally be considered as a type of natural enclosure. The mounds are generally situated in a grassy area and are surrounded by a low wall of earth. The mounds are generally situated in a grassy area and are surrounded by a low wall of earth. The mounds are generally situated in a grassy area and are surrounded by a low wall of earth.

It is probable that these mounds were built by birds. The mounds are generally situated in a grassy area and are surrounded by a low wall of earth. The mounds are generally situated in a grassy area and are surrounded by a low wall of earth.

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CHAPTER 6

GENERAL DISCUSSION

6.1 Functional differences between mounds and intermounds

The mounds studied generally agreed with the descriptive features of Mima mounds given in Chapter 1. However, certain aspects of possible interactions between termites and fossorial rodents in regard to mound origin were found. There was more clay on the mound surface soils than on the intermounds, a characteristic normally associated with termite mounds (Hesse 1955). Many mounds exhibiting mole-rat activity were occupied by termites, and in some cases, termite foraging tunnels and ventilation shafts were found on mound tops.

It is probable that these mounds were made by mole rats or termites or both. Whichever the case, mounds would be expected to attract both mole rats and termites as the foraging strategy of both animals is probably to search for food items that maximise dietary gains at minimum cost.

To end this controversy, further research should be planned to verify mound origin in this area, particularly because the mounds occur in a zone inhabited by both mole rats and termites.

This study, with the primary purpose of examining the interaction between herbivorous mammals and mound and intermound vegetation, provides insight into the functional significance of mounds in grasslands. Soil differences form the basis from which all other characteristics of mound and intermound differences stem. Mound soils were of better textural qualities, higher plant nutrient levels, and had pH ranges that were more agreeable to plant growth than intermounds.

The mounds, with a more heterogenous botanical composition, should provide a greater diversity of food items to grazers. They should also provide more forage for grazers, as they have higher net primary production than intermounds, especially during the rainy seasons. The higher decomposition rate of mound vegetation

during the dry season implies a higher rate of nutrient cycling.

The differences in food utilization by grazers between mound and intermound vegetation may have a cyclic effect, as grazers are known to influence the amount, rate of production, quality of food available to them, and composition and diversity of vegetation (McNaughton 1985), properties that enhance plant functional responses to grazing.

The net nutrient gains of grazing animals would be enhanced by concentrating on mounded areas which have higher forage quality. However, forage potentially available to herbivores during the dry seasons can be substantial, but its occurrence in time and space is highly variable compared to the intermounds which are characterised by high standing crop of dry, poorer quality forage that is less readily eaten by herbivores.

The higher crude protein content and lower death rate of mound vegetation show that they provide forage that is more acceptable to grazers than the intermounds, even during the dry season when forage quality drops.

Herbivores spend more time feeding on mounds than on intermounds. Assuming that dung deposition is proportional to the time animals spend in each habitat, the grazers act as nutrient concentrators, harvesting nutrients over large areas and concentrating them on smaller areas, a factor that increases nutrients in the mound soils.

6.2 Importance of mounded grasslands

Mounds, with their deeper soils, more favourable moisture relations and higher fertility, yield greater production of higher nutrient quality forage that retain good herbage for wild animals later into the dry season than intermounds. Their grazing value to the domestic animals has also been reported (Scott 1963).

Some peasant farmers in dry areas immediately west of Thika town cultivate on mounds during the short rainy season, leaving the intermound fallow. Stephen *et al.* (1956) and Scott (1963) observed that the Thika and Athi-Kapiti mounds

produced better growth of maize and sisal when put into cultivation. Gakahu (personal communication) has noted that mounds around Eldoret produce more vigorously growing wheat than intermound areas. Trees at elevations of 1800 - 1950 m near north of River Trans-Nzoia, showed a strong tendency to be restricted to mound areas (Troll 1936).

The conservational importance of mounded topography has been described in Chapter 1. In Kenya, no area has been accorded the status of a National Park or Game Reserve solely because of the presence of mounds. It is hoped that the findings of this study will be put into practical consideration by our planners in the protected game areas. In Kenya, there is a tendency to construct roads and lodges in areas of high animal density. The study area has a high network of roads and off-road driving is rampant, as most parts are accessible by vehicle. During the dry season, animals are disturbed by tourists and vegetation destroyed by off-road driving. As these areas provide good forage during the dry season, they should be accorded protective management measures by reducing the number of roads through them and enforcing the ban on off-road driving, steps that would minimise disturbance of animals and destruction of vegetation.

In Nairobi National Park, over 14 dams have been constructed, most of them near the roads, presumably to lure animals for tourist viewing. In the study area where animals are plentiful, no dams have been constructed, and the area continues to be a dry season concentration area for animals. In the mounded area near the Hyena dam, about 8 km west of the study area, the mounded grasslands have failed to be of critical value to the grazers, since instead of providing food far into the dry season, the animals converge at the water source, deplete most of the vegetation available, leaving very little for use as the dry season intensifies. It should be the practise of planners that in areas where mounds occur in natural grazing areas, infrastructures that would alter the grazing pattern of herbivores should be minimised or avoided.

Since the mounds are high potential areas relative to the adjacent intermounds, they should be put into proper land-use management plans in all the localities in which they occur.

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A P P E N D I X

Plants sampled in mounds only (Group A) intermounds only (Group B) and those common to both mounds and intermounds (Group C).

GROUP A

Graminoids

1. *Aristida adoensis*
2. *Aristida Keniensis*
3. *Eragrostis cilianensis*
4. *Panicum maximum*
5. *Setaria sphacelata*
6. *Commelina benghalensis*
7. *Commelina reptans*

Shrubs

1. *Abuliton mauritianum*
2. *Crotalaria pycnocephala*
3. *Grewia similis*
4. *Lantana trifolio*
5. *Leonotis nipetifolia*
6. *Scurtia myrtina*

Forbs

1. *Alysicarpus rugosus*
2. *Asystacia schimperi*
3. *Agelatum conysoides*
4. *Achyranthes aspera*
5. *Calylusea abyssinica*
6. *Corchorus tridentata*
7. *Cordions tuloculans*
8. *Dactyloctenium aegypticum*
9. *Dolichos luticola*
10. *Euphorbia hirta*
11. *Emilia coccina*
12. *Erucastrum arabicum*
13. *Fibristylis monstachya*

Forbs Cont'

14. Helichrysum glumaceum
15. Ipomea obscura
16. Ipomea polymorpha
17. Redrostis foetidissima
18. Leucas grabrata
19. Leucas marticonsii
20. Laurea cornuta
21. Newtonia johnstonii
22. Oxygonum sinuatum
23. Osimum suave
24. Portulaca oleracea
25. Polygala erioptera
26. Schkuhria pinnata
27. Sonchus exauriculatus
28. Senecio defacifolium
29. Scurtia myrtina
30. Talium portulacifolium
31. Zaleya pentandra

GROUP B

Graminoids

1. Chrysopogon aucheri
2. Eragrostis superba
3. Heteropogon contortus
4. Microchloa Kunthii
5. Rhynchelytrum repens
6. Hypoxis angustifolia

Shrubs

1. Acacia drepanolobium
2. Carrisa edulis

Forbs

1. Aster lussopifolius
2. Anthericum gregozianum

Forbs Cont'

3. *Alysicarpus eranthemoides*
4. *Blepharis fruticosa*
5. *Chlorophytum micranthum*
6. *Gutenbergia callysina*
7. *Leucas neuflyzeana*
8. *Ormithogulon caudatum*
9. *Orthosiphon pervifolius*
10. *Ormocarpus tricocarpum*
11. *Ormocarpus kirkii*
12. *Osteopermum railantii*
13. *Paxonia urens*
14. *Thunbergia sericea*

GROUP C

Graminoids

1. *Bothriochloa insculpta*
2. *Bracharia viridula*
3. *Cenchrus ciliaris*
4. *Cymbopogon caseus*
5. *Cymbopogon pospischilii*
6. *Cynodon dactylon*
7. *Digitaria Scalarum*
8. *Digitaria macroblephara*
9. *Eragrostis tenuifolia*
10. *Eustachys paspaloides*
11. *Harpachne schimperii*
12. *Ischaemum afrum*
13. *Panicum pogoides*
14. *Pennisetum mezianum*
15. *Pennisetum stramineum*
16. *Setaria pallidifusca*
17. *Sporobolus pyramidalis*
18. *Sporobolus marginatus*
19. *Sporobolus pellucidus*
20. *Setaria sphacelata*
21. *Themeda triandra*
22. *Commelina africana*
23. *Pennisetum Schimperii*

Shrubs

1. *Aspilia mosambicensis*
2. *Acacia brevispica*
3. *Cassia mimosoidae*
4. *Capparis fasciculatus*
5. *Grewia bicolor*
6. *Grewia tembensis*
7. *Hibiscus aponeurus*
8. *Hibiscus flavifolius*
9. *Jasminium flumescence*
10. *Lippia javanica*
11. *Nesaea Iythroides*
12. *Solanum incanum*

Forbs

1. *Asperagus africanus*
2. *Antheroisma psylloides*
3. *Becium obovatum*
4. *Bidens pilosa*
5. *Barleria eranthemoides*
6. *Convolvulus sagittatus*
7. *Conyza parrhopappa*
8. *Conyza stricta*
9. *Cucumis esculeatus*
10. *Crossandra subacaulis*
11. *Cynoglossum caeruleum*
12. *Dyschoriste radicans*
13. *Euphorbia inaequilatera*
14. *Evolvulus alanoides*
15. *Enicostema hissopifolium*
16. *Gutenbergie cordifolia*
17. *Indegofera volkensisii*
18. *Indegofera triata*
19. *Justacia whittii*
20. *Lactuca capensis*
21. *Laggera briveps*
22. *Monechma debile*

Forbs Cont'

23. *Monsonia longipes*
24. *Melhania ovata*
25. *Oldenlandia johnstonii*
26. *Phyllanthus maderaspatensis*
27. *Pentanisia ouronygne*
28. *Psilotrichum schimperi*
29. *Plectrunthus caninus*
30. *Priva curtisiae*
31. *Pellea viridis*
32. *Rhynchosia minima*
33. *Ruellia patula*
34. *Sida ovata*
35. *Sida ocuta*
36. *Tagetes minuta*
37. *Tephrosia hildebrandtii*
38. *Vigna schimperi*

Others

1. *Kyllinga leucocephala*
2. *Cyperus giolii*